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QUANTITATIVE ANALYSIS OF THE ECOLOGICAL DISTRIBUTION OF A TROPICAL HERPETOFAUNA

By

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INTRODUCTION

Possibly the rainforest environment is not so constant, equitable, and predictable as ecologists have assumed. Lloyd, Inger, and King (1968) suggested this possibility as a result of studies on amphibian and reptile diversity in tropical rainforests of Borneo. The ways in which species utilize environmental resources have long been of interest in ecology; recently some effort has been made to analyze the inherent properties of the rainforests as they relate to amphibians and reptiles. Schoener (1970) studied nonsynchronous spatial overlap of lizards, genus *Anolis*, in patchy habitats in the West Indies. Schoener and Gorman (1968) studied niche differences of three species of *Anolis* from the southern Lesser Antilles; Schoener (1968) also studied resource partitioning among anoles on South Bimini Island. Rand (1964) examined the ecological distribution of anoles in Puerto Rico. Rand and Humphrey (1968) studied ecological distribution and interspecific competition among lizards in the rainforest at Belém, Brasil. Duellman (1967) studied isolating mechanisms and resource partitioning in tree frogs in Costa Rica. Inger and Greenberg (1966) studied the relation between niche overlap and interspecific competition for three species of frogs, genus *Rana*, in Sarawak. As indicated, the majority of studies have been carried out on specific genera; no extensive, quan-

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titative ecological studies have been carried out in the New World tropics on an entire reptilian or amphibian community.

This is a report on the ecological distribution of amphibians and reptiles undertaken at the Guamá Ecological Research Area near Belém, Brasil. Field work was carried out from mid-January through July 1969, in April 1970, and in June and July 1970. Part of the resultant collection was given to the Museu Goeldi in Belém, and part is catalogued in the Museum of Natural History at the University of Kansas.

The objectives of the present study are threefold: 1) to determine the ecological distribution of 62 species of frogs, salamanders, and lizards within the rainforest environment of Belém; 2) to analyze the environmental parameters affecting the distribution of species; and 3) to compare and contrast the major areas with regard to species composition. The ecological distribution of the herpetofauna presented here is based on data obtained in one small area in part of the year. A similar study carried out from August through January or in a different area probably would yield somewhat different results.

DESCRIPTION OF THE AREA

Belém is located about one degree south of the equator, in the lower Amazon Basin, Estado do Pará, Brasil; the elevation at the highest point is 12 m above sea level. The mean annual temperature is 26°C, and the average monthly temperature varies less than 2°C throughout the year. Seasonality is reflected through the temporal distribution of rainfall, yielding wet and dry seasons. The average annual rainfall (44 years) for the wet season, January through June, at Belém is 2028 mm, whereas that for the dry season, July through December, is 830 mm (Belém Virus Laboratory, 1967 Annual Report).

Belém is the headquarters for the Instituto de Pesquisas e Experimentação Agronomicas do Norte (IPEAN). An area of about 310 hectares of IPEAN property has been designated as the Guamá Ecological Research Area (APEG). Most of my study was carried out in two of the APEG reserves. The Aurá Reserve is part capoeira, part terra firme (Fig. 1), and part varzea forest (Fig. 2); some areas are transitional between terra firme and varzea forests. The Catú Reserve is a transect of igapó forest (Fig. 3) 1000×200 m. See figure 4 for spatial relationship of the reserves. The forest types are defined below.

The reserves are divided into a network of 10×10 m quadrats, each marked with a numbered stake. For each observation or in-



FIG. 1. Terra firme forest (Aurá reserve). Well-drained forest on relatively high ground. Photo by Roger Arle.



FIG. 2. Varzea forest (Auré reserve). Flooded daily by the back-up from the Rio Guamá; predominance of Acai palm trees (*Euterpe oleracea*). Photo by Roger Arle.



FIG. 3. Igapó forest (Catú reserve). Permanently flooded forest. The boardwalk provides easy access.

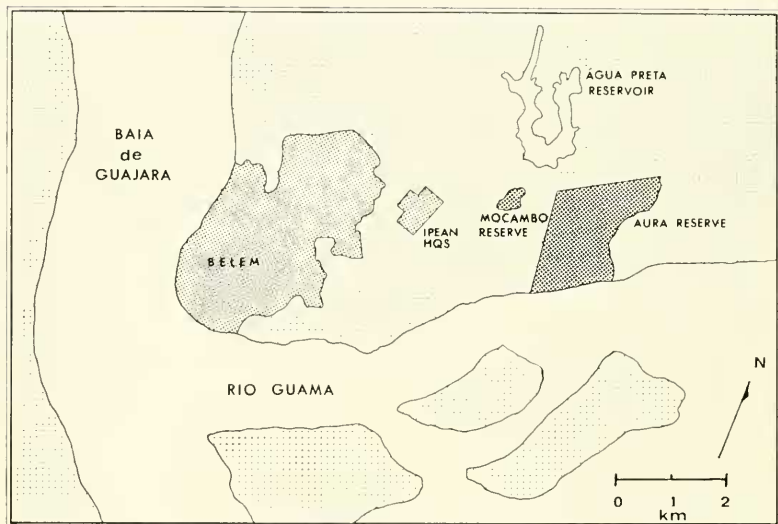


FIG. 4. Map of Mocambo and Aurá Reserves in relation to Belém and the Rio Guamá. The Mocambo Reserve consists of terra firme forest, surrounded by the Catú reserve of igapó forest (not indicated on map); the Aurá Reserve consists of terra firme, capoeira, varzea, and transition forest areas. Some studies were carried out in the vicinity of the IPEAN headquarters and at the Agua Preta Reservoir (Utinga Reserve).

dividual collected, the hectare and quadrat numbers were recorded, thereby assuring that all data were collected in the same spatial frame of reference. The distribution of water was determined and mapped for the capoeira, terra firme, and varzea study areas (Figs. 5-9); species distributions were superimposed on these maps to determine the associations of species with standing water. For the various quantitative analyses, 44 sampling plots, each 20×30 m, from four of the major forest areas were studied. The location of the 4 capoeira-terra firme transition, 19 terra firme-varzea transition, and 9 varzea plots relative to each other and to the distribution of water is shown in figures 10 and 11. The other 12 plots were in the igapó forest. For the purpose of an analysis of ecological distribution, the rainforest at Belém was divided into seven major areas:

Terra firme forest.—Well-drained forest on relatively high ground that is never subject to flooding is called terra firme forest. It is a well-structured, complex, tropical rainforest. One 5.5 hectare area of terra firme forest (Mocambo Reserve) has been studied extensively by botanists. Cain *et al* (1956) found the area to be extremely complex, both in vegetation species richness and in vegetation density; they estimated the density of trees exceeding 10 cm

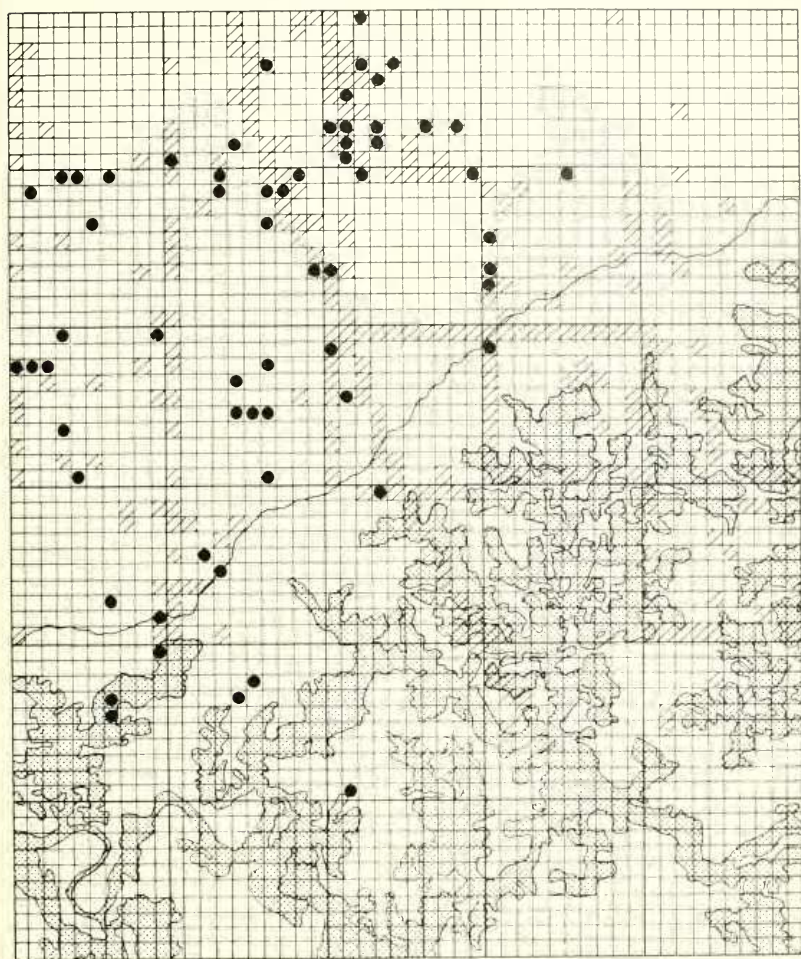


FIG. 5. Distribution of *Bolitoglossa altamazonica* in relation to distribution of water in terra firme, capoeira, and varzea transition forest. Each small square represents a quadrat, 10 x 10 m. Cross-hatched quadrats are those areas in which at least one frog, salamander, or lizard was observed by the author. Stippled areas represent terra firme-varzea transition depressions filled with standing water; non-stippled areas are better drained and usually are located on higher ground. Each dot represents the observation of at least one individual of *Bolitoglossa altamazonica* within the particular quadrat.

in diameter to be 594 trees per hectare. Dr. Murca Pires, a botanist associated with IPEAN, identified 215 species of trees in this area. Hatheway (1967) estimated the canopy to be 80 percent closed, with an average canopy height of about 35 m. He distinguished three strata of vegetation. Beneath the nearly closed canopy is a

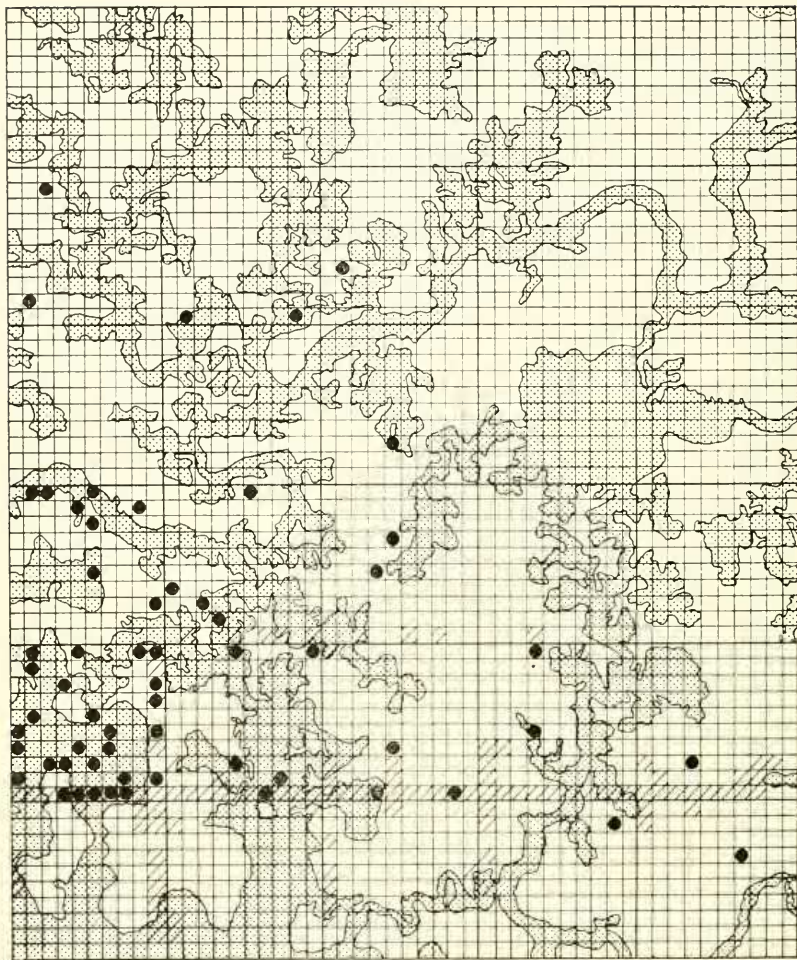


FIG. 6. Distribution of *Bolitoglossa altamazonica* in relation to distribution of water in varzea forest. See figure 5 for explanation; in this figure stippled areas represent varzea depressions filled with standing water.

deep layer of trees up to 20 m in height; the bottom, dense, scrubby layer extends to a height of about 1.5 m from the ground.

Varzea forest.—Swamp forest bordering the rivers is known locally as varzea. This forest is flooded daily by the back-up of the Rio Guamá, due to tidal effect. The degree of flooding varies throughout the year and is correlated with rainfall. All aquatic environments in the immediate vicinity of Belém seem to be fresh-water (Humphrey, pers. com.). The “white water,” so called because of the presence of sand, silt, and clay particles, yields a con-

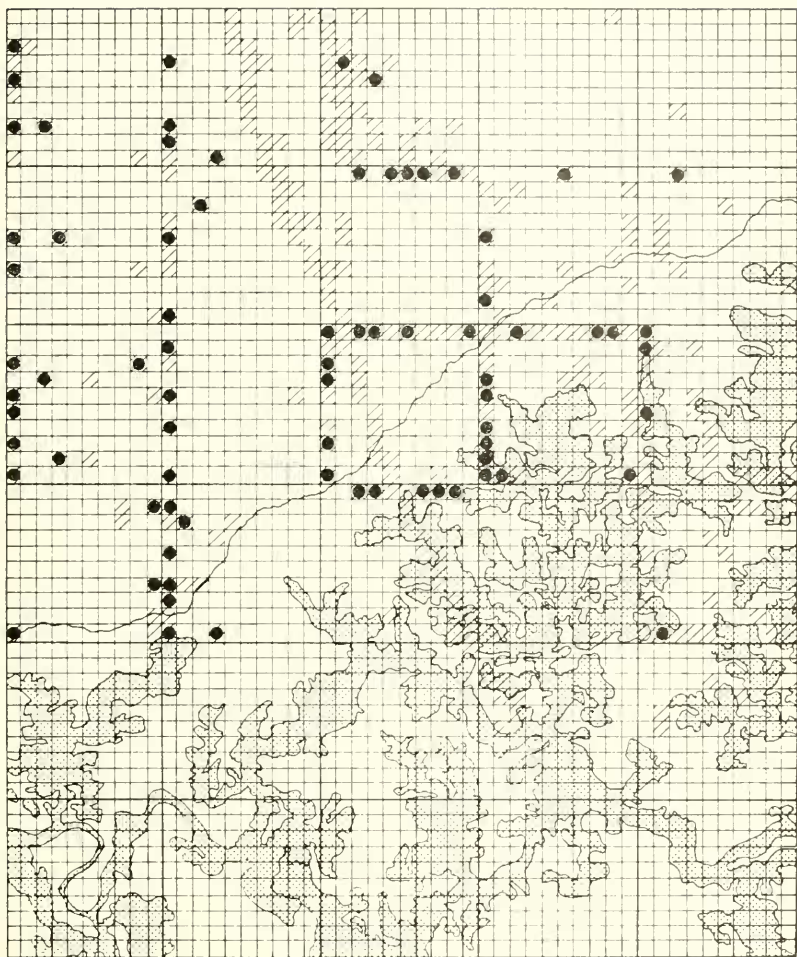


FIG. 7. Distribution of *Leptodactylus marmoratus* in relation to distribution of water in terra firme, capoeira, and varzea transition forest. See figure 5 for explanation of symbols.

tinual deposition of alluvium. The resultant alluvial varzea soil is rich, but has a low permeability. During the rainy season, parts of the varzea are flooded to a depth of 1 m or more. Depressions are present, resulting in differential drainage. Tall woody plants, palms, and giant aquatic herbs exist nearly side by side as a consequence of drainage patterns (Hatheway, 1967). There is a predominance of palms in the varzea forest; the acai palm (*Euterpe oleracea*) is the most common tree. Lianas and epiphytes are common, and moss as thick as 1 cm covers the trunks of trees up to 2 m

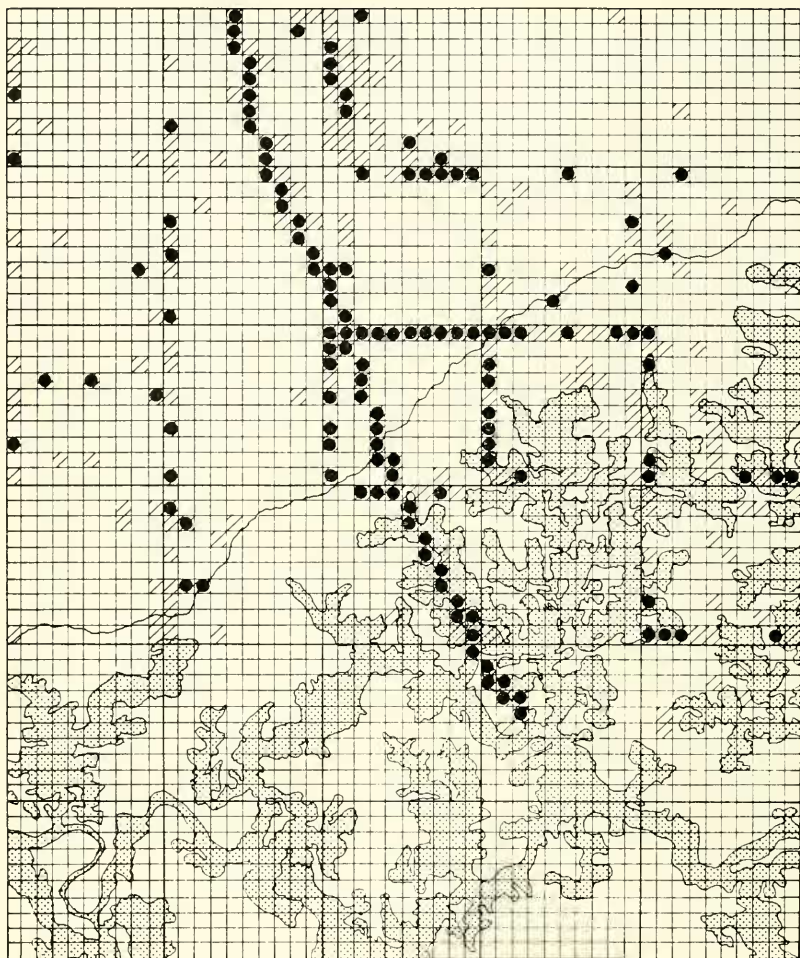


FIG. 8. Distribution of *Gonatodes humeralis* in relation to distribution of water in terra firme, capoeira, and varzea transition forest. See figure 5 for explanation of symbols.

from the ground. Hatheway (1967) proposed that epiphytic mosses likely indicate high humidity in tropical forests. In the varzea, this high humidity probably results from constant evaporation from the moist ground and water. Hatheway estimated that the total density of trees over 10 cm in diameter is probably greater than 600 trees per hectare. The canopy is about 50 percent open, and the canopy trees are 30-35 m in height.

Igapó forest.—This is forest that is permanently flooded with “black water,” so called because of organic residues. Hatheway

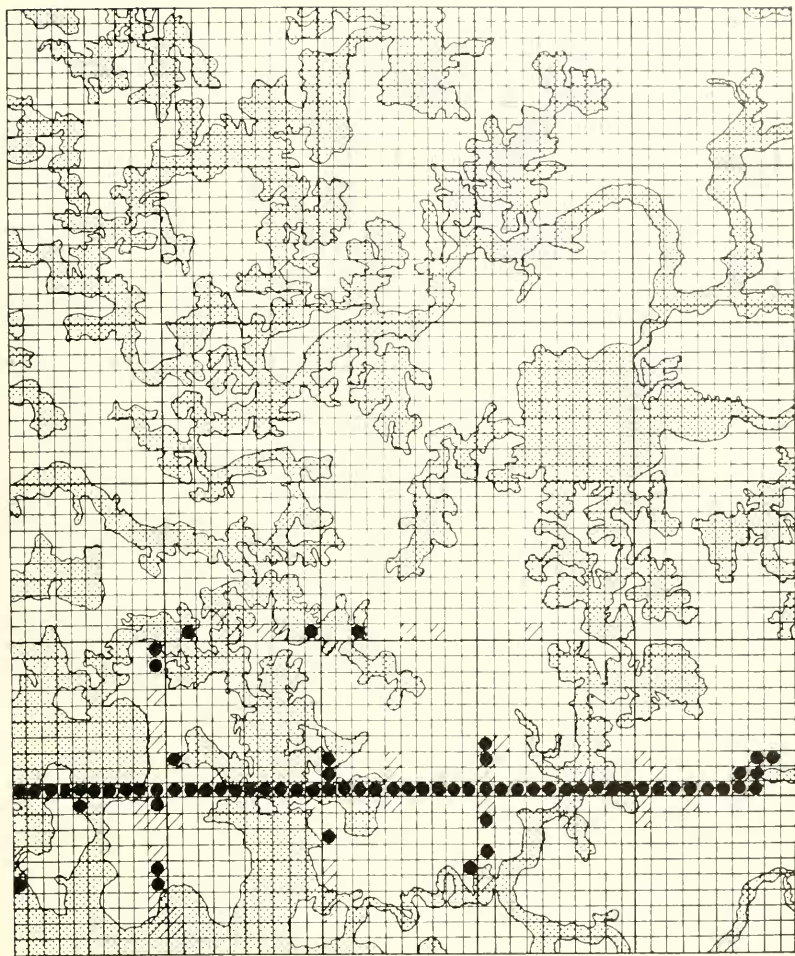


FIG. 9. Distribution of *Gonatodes humeralis* in relation to distribution of water in varzea forest. See figure 6 for explanation of symbols.

(1967) estimated the average depth of water to be 25 cm; beneath the water is another 25 cm of organic, water-logged muck, underneath which is white clay. The area consists of many stagnant, foul-smelling, interconnected pools. Small islands of root masses project from the pools; much of the vegetation in the swamp forest is supported on these islands, although a few trees are rooted in the muck. There is no well-formed canopy, and other distinct vegetational layers are difficult to distinguish. Most trees are small-crowned, slender dicots, rising above the thick mesh of tangled roots elevated to 3 m above the deep mud of the swamp.

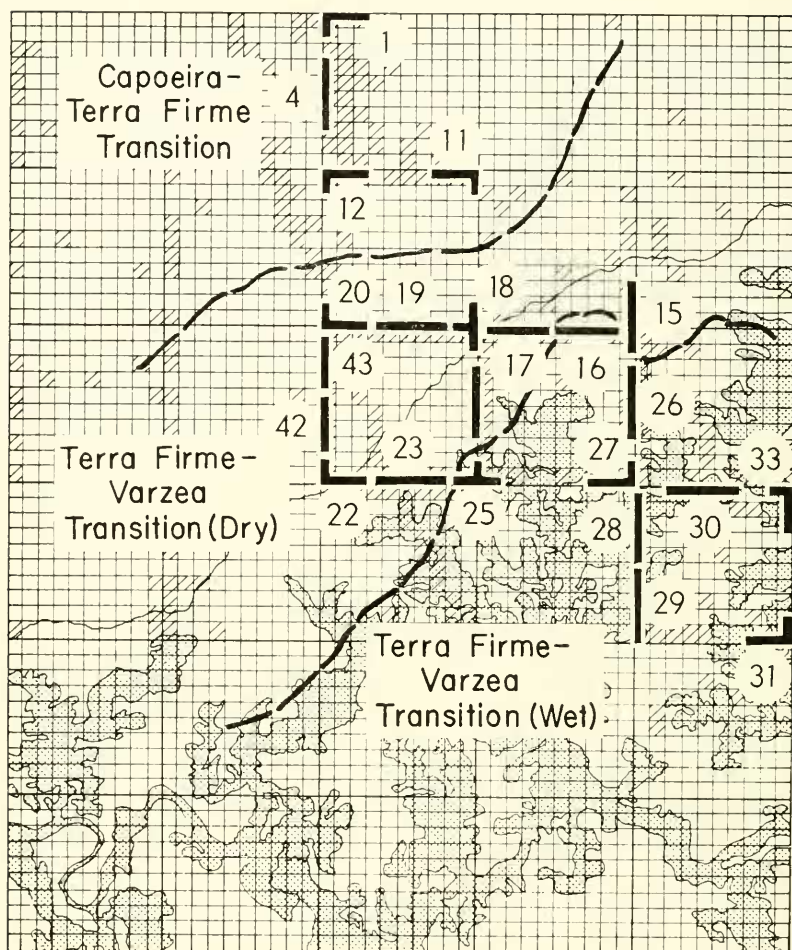


FIG. 10. Distribution of sampling plots in relation to distribution of water in terra firme, capoeira, and varzea transition forest. See figure 5 for explanation of symbols. The numbered plots, each 20 x 30 m, are indicated by heavy, straight lines; data from these plots were used in the contingency table analysis.

Capoeira forest.—This is second growth forest on well-drained ground. The capoeira areas studied had relatively open canopies and fairly dense ground cover. Much of the area is composed of tall grasses and ferns; the forest floor in some sections is covered with brush and fallen logs.

Capoeira-terra firme transition.—Four plots were studied which are intermediate between capoeira and terra firme forest with re-

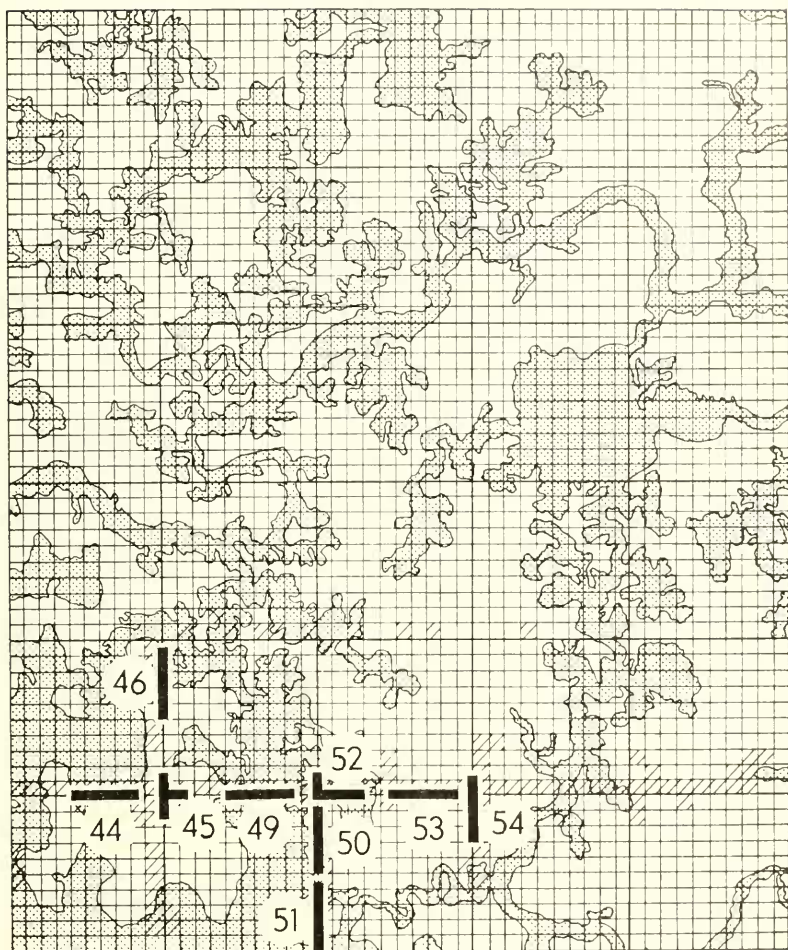


FIG. 11. Distribution of sampling plots in relation to distribution of water in varzea forest. See figures 6 and 10 for explanation.

gard to characteristics of canopy and ground cover. The plots exhibit a greater vegetation density than typical capoeira, but less than typical terra firme forest.

Terra firme-varzea transition.—Plots in one area exhibit some characteristics of both terra firme and varzea forests, but differ noticeably in other ways. For instance, on well-drained ground there is a lower vegetation density than in typical terra firme forest. The flooded portion lacks the predominance of palms, characteristic of typical varzea forest. Corresponding to the varzea and terra firme forests respectively, some of the soil in the transition area is

a poorly-drained, silty-clay alluvium, whereas other soil is a well-drained, heavy, yellow laterite.

Open and edge.—All non-forest study sites are grouped in this category. Observations and collections were made in swampy areas in open fields, ponds along forest edges, and in second growth vegetation bordering the IPEAN reserves. During the rainy season, the swamps and ponds contained water to a depth of about 1 m but were usually less than half as full during June and July. Dirt roads and roadside ditches on IPEAN property and sewage swamps within the city were examined weekly.

COMPOSITION OF THE HERPETOFAUNA

Three orders of amphibians: Gymnophiona (caecilians), Caudata (salamanders), and Anura (frogs) and four orders of reptiles: Amphisbaenia (amphisbaenids), Crocodilia (crocodilians), Squamata (lizards and snakes), and Testudines (turtles) are represented in the herpetofauna (116 species) of the Belém area; amphibians represent 35.4 percent of the herpetofauna, and reptiles 64.6 percent. The breakdown of species is as follows: caecilians—3, salamanders—1, frogs—37, amphisbaenids—3, crocodilians—1, lizards—24, snakes—44, and turtles—3. Further field work probably will reveal several additional species of snakes, caecilians, and turtles, as well as species of other groups.

METHODS

Most observations and collections in the forests were made along paths and boardwalks constructed several years previously. Therefore, the data are biased to whatever extent the different species are influenced by the narrow, open areas maintained by continuous human activity. Species distributions necessarily reflect my sampling activity (Figs. 5-9).

An approximately equal amount of field work was done by day and by night. Every frog, salamander, and lizard observed was recorded by species, date, and locality (including hectare and quadrat numbers from the labeled study areas). The distribution of each of the 62 species was plotted on quadrat maps. Although snakes, turtles, and caecilians were collected, the few numbers of specimens of these groups precluded their inclusion in the analyses. Environmental gradients affecting the distribution of species within four major forest areas was inferred by use of a contingency table analysis. Resource partitioning was studied by means of field observations and analyzed by niche breadth and niche overlap anal-

yses. Following the analysis of species distributions, the species compositions of the major areas were compared and contrasted by means of the Shannon species diversity formula, an equitability index, and coefficients of communities (see appropriate sections).

Definitions of terms, as I am using them, and a brief discussion of techniques of analysis are given below. The analytical techniques are treated in detail in appropriate subsequent sections of this paper.

Major areas.—The region studied can be divided into several geographical sections referred to as major areas. I have delimited the artificial boundaries in such a way that each area possesses a certain subjective uniformity with regard to physical environmental parameters, such as vegetational physiognomy, light intensity, water, and soil type. The quantitative analyses were carried out on data obtained from four major forest areas: 1) capoeira-terra firme transition; 2) terra firme-varzea transition; 3) varzea; and 4) igapó. Resource partitioning observations were carried out in the following major areas: 1) open and edge; 2) capoeira; 3) terra firme; 4) varzea; and 5) igapó.

Habitat.—This term refers to the structural aspect of a niche; it is that portion of the physical environment in which an organism carries out its life processes. The physical environment supports species in three major ways: 1) vertical zonation; 2) horizontal distribution; and 3) temporal spacing.

Community.—A community consists of interacting populations of animals. Each of the major areas included in this analysis has a herpetofaunal community different from every other area. The interaction and organization of each community is expressed in terms of resource partitioning with regard to differential utilization of the environment in space and time, species diversity including both species richness and equitability components, and species composition and relative abundance.

Resource partitioning.—This term refers to the differential utilization of the physical environment in space and time by different species. The result of resource partitioning is highly efficient utilization of environmental resources.

Niche.—This is an abstract concept referring to the habitat and biotic relationships of an animal. A niche can be thought of as a hypervolume, consisting of numerous dimensions (Hutchinson, 1957); the dimensions are physical factors and biotic relationships required by a species for survival. The physical factors of the environment making up the structural component (habitat) of the niche exist independent of the species, but the entire niche, inclusive of the position (biotic relationship) of the animal, does not exist

independent of the species. Therefore, the niche is a function of the species. Formation of a particular niche is ultimately dependent on the structural adaptations, physiological requirements and capabilities, and correlated behavioral patterns of the species. No two species have identical physical and biotic requirements, coupled with identical structural, physiological, and behavioral attributes, and therefore no two species have the same niche.

Niche breadth.—This term is used to describe the spectrum of any given dimension of the niche hypervolume. For instance, one can speak of the food preference niche breadth of species A and B. If species A eats 10 different kinds of insects and species B eats only 2 kinds of insects, species A is said to have a broad food preference niche breadth and species B a narrow food preference niche breadth relative to each other. Niche breadth as used in this paper refers to the habitat niche breadth.

Niche overlap.—This term refers to the situation in which two or more species have similar requirements with respect to some dimension of the niche hypervolume. Niche overlap is a measure of the association of two or more species. The measurements in this study were obtained indirectly by the degree of coexistence of the species in the various plots sampled.

Habitat-generalists, intermediates, and specialists.—Habitat-generalists are species that utilize a broad spectrum of the environment, as indicated by the contingency table indices; they are found in all four major forest areas and have high habitat niche breadth scores (16.0-32.0), as calculated from Levins' index. Habitat-specialists are species apparently restricted in their distributions to one or two of the major forest areas; they seem to live in a narrow range of the environmental spectrum and have low niche breadth scores (1.0-4.0). All other species are referred to as habitat-intermediates. In most instances, the habitat-specialists are the least common species, whereas the habitat-generalists are the most abundant.

Species diversity.—The concept of species diversity consists of two components, species richness and equitability. The former is the number of species, and the latter is the evenness with which the individuals are distributed among the species. A community having a large number of species in which the abundance decreases gradually from the most to the least abundant species is considered to have a high species diversity. According to Whittaker (1970), niche differentiation results in greater species richness through time, whereas a narrowing of habitat distributions tends to increase species equitability. Some investigators propose that species richness depends primarily on the structural diversity of the habitat, whereas

equitability is more dependent on the stability of physical conditions. Apparently the more complex the vegetation is vertically, the greater is bird species diversity (MacArthur and MacArthur, 1961; MacArthur, MacArthur, and Preer, 1962; MacArthur, 1964, 1965; and MacArthur, Recher, and Cody, 1966). Pianka (1967) proposed that spatial heterogeneity is the most important single factor determining the number of species of lizards in any given area. One of the most commonly accepted formulas to measure species diversity is the Shannon function (Shannon, 1948). Pielou (1966) discussed its use and disuse. The formula is used to describe an infinitely large population and results in the average diversity per species.

Coefficient of community.—The coefficient of community (CC) is a mathematical measure of relative similarity of samples from two communities (Whittaker, 1970).

ANALYSIS OF ECOLOGICAL DISTRIBUTION

As discussed in the preceding section, each major area is a complex of intrinsic physical environmental parameters, different from those in other areas. Each species is adapted to a particular range of each environmental gradient; the totality of environmental gradients forms the structural niche, or habitat, of the species. One must assume that habitat adaptation is based on the genetic make-up of the individuals of the species in terms of morphology, physiology, behavior, and life cycle. Based on the preceding assumptions, the following hypothesis can be stated: The 62 species of frogs, salamanders, and lizards in the Belém area are distributed in such a manner that environmental resources are partitioned; the consequence of habitat differentiation is highly efficient utilization of the environment.

Several techniques were used to study the ecological distribution and to test the hypothesis; others were used to compare and contrast the species composition within each major area. To avoid confusion, each analysis is presented separately. Included in each section is an explanation of purpose and a presentation and discussion of results; where applicable, advantages and limitations of the analyses are indicated.

The distribution of frogs, salamanders, and lizards as taxonomic groups within five of the major habitats is presented in table 1. The varzea has the highest species richness, with 38 (61.3%) of the 62 species occurring there. Next in terms of species richness is terra firme forest, with 36 species (58.1%). The area with the lowest value is capocira, with only 20 species (32.2%). The mature forest

TABLE 1.—Distribution of Amphibians and Lizards by Major Taxonomic Groups in Five of the Major Areas. The top numbers are the number of species of a taxonomic group in a given area; percentages are the proportion of the taxonomic group in the area. Numbers in parentheses indicate the sum of the coded relative abundance indices (Table 2) for the taxonomic group in the area.

Group	Terra Firme	Varzea	Igapó	Capoeira	Open & Edge
Frogs and toads	20	22	13	8	24
37 species	54.0% (36)	59.4% (56)	35.1% (23)	21.6% (12)	64.9% (80)
Salamanders	1	1	1	1	0
1 species	100% (4)	100% (4)	100% (2)	100% (3)
Lizards	15	15	8	11	10
24 species	62.5% (27)	62.5% (29)	33.3% (16)	45.8% (19)	41.7% (23)
Total No. Species	36	38	22	20	34
% Total Species (62)	58.1%	61.3%	35.5%	32.2%	54.8%
Sum Abundance Indices	67	89	41	34	103
Average Species					
Abundance Index	1.86	2.34	1.86	1.70	3.03

areas likely are highest in species richness due to the greater vegetational diversity, yielding environmental heterogeneity, as contrasted to second growth areas (capoeira) having less structural complexity. Open and edge areas are relatively rich with 34 species (54.8%); 24 species of frogs (62.3% of the total anuran fauna) breed in the numerous ponds in these areas. Abundance indices for each species in each area were coded as follows: 0=apparently absent (none observed); 1=not commonly seen (1-4 observations); 2=moderately common (5-15); 3=common (16-25); and 4=abundant (26 or more observations). The average abundance index (obtained by dividing the sum of the abundance indices for all the species in a given area by the total number of species in that area) is much higher in open and edge areas (3.03) than the next highest which is the varzea forest (2.34); this is partially due to the large congregations of breeding frogs in open and edge areas. In addition, population densities of lizards are higher in open areas than in the forest, although this may be due to censusing methods; lizards are more easily seen in open and edge areas than in the dense forest. The ecological distribution and relative abundance of each species of frog, salamander, and lizard are shown in table 2. It is evident that certain species have a much broader range of ecological distribution than do others. Figures 5-9 indicate the distribution of three species relative to the distribution of water. The salamander, *Bolitoglossa*

TABLE 2.—Ecological Distribution of Frogs, Salamanders, and Lizards. Numbers indicate relative abundance of a species within an area, coded 0-4 as follows: 0=Apparently absent (none observed), 1=Not commonly seen (1-4 observations), 2=Moderately common (5-15), 3=Common (16-25), and 4=Abundant (26 or more observations).

Species	Terra Firme	Varzea	Igapó	Capoeira	Open & Edge
<i>Pipa pipa</i>	0	1	0	0	0
<i>Eleutherodactylus lacrimosus</i> ..	1	0	1	0	0
<i>Leptodactylus marmoratus</i>	4	4	0	3	0
<i>Leptodactylus mystaceus</i>	1	0	0	0	0
<i>Leptodactylus ocellatus</i>	0	0	0	0	4
<i>Leptodactylus pentadactylus</i> ..	1	0	0	0	0
<i>Leptodactylus rhodomystax</i>	1	2	0	0	0
<i>Leptodactylus wagneri</i>	1	4	4	0	2
<i>Physalaemus ephippifer</i>	4	4	1	1	4
<i>Physalaemus petersi</i>	3	4	0	0	2
<i>Bufo marinus</i>	0	0	0	0	4
<i>Bufo typhonius</i>	4	4	0	2	0
<i>Dendrobates trivittatus</i>	2	0	0	1	0
<i>Dendrobates ventrimaculatus</i> ..	0	2	3	0	0
<i>Hyla baumgardneri</i>	0	0	1	0	4
<i>Hyla boesemani</i>	0	0	0	0	4
<i>Hyla calcarata</i>	1	3	0	0	0
<i>Hyla egleri</i>	2	3	2	1	4
<i>Hyla geographica</i>	0	4	0	0	2
<i>Hyla goughi</i>	1	2	1	0	4
<i>Hyla granosa</i>	1	2	3	0	0
<i>Hyla leucophyllata</i>	0	2	1	0	4
<i>Hyla melanargyrea</i>	1	0	0	0	4
<i>Hyla minuta</i>	0	0	0	0	4
<i>Hyla multifasciata</i>	0	2	1	0	4
<i>Hyla nana</i>	1	0	0	0	4
<i>Hyla raniceps</i>	0	1	0	0	4
<i>Hyla rondoniae</i>	0	1	0	0	0
<i>Hyla rubra</i>	1	3	3	1	4
<i>Hyla</i> sp. (large <i>rubra</i>)	1	1	0	0	4
<i>Hyla</i> sp. (<i>rubra</i> -like)	4	4	1	2	1
<i>Osteocephalus taurinus</i>	0	0	0	0	1
<i>Phrynomidas venulosa</i>	1	0	1	1	3
<i>Phyllomedusa bicolor</i>	0	2	0	0	2
<i>Phyllomedusa hypochondrialis</i> 0	0	0	0	0	4
<i>Phyllomedusa vaillanti</i>	0	1	0	0	0
<i>Sphaenorhynchus eurhostus</i>	0	0	0	0	3
<i>Bolitoglossa altamazonica</i>	4	4	2	3	0
<i>Gonatodes humeralis</i>	4	4	3	3	0
<i>Hemidactylus mabouia</i>	0	0	0	0	4
<i>Thecadactylus rapicaudus</i>	1	0	0	0	0
<i>Lepidoblepharus festae</i>	0	1	1	0	0
<i>Anolis fuscoauratus</i>	3	3	1	1	0
<i>Anolis ortonii</i>	1	0	0	0	0
<i>Anolis punctatus</i>	1	1	0	1	0
<i>Iguana iguana</i>	0	1	0	0	1
<i>Plica umbra</i>	3	1	1	2	0
<i>Polychrus marmoratus</i>	1	1	1	1	0

TABLE 2.—(Concluded)

Species	Terra Firme	Varzea	Igapó	Capoeira	Open & Edge
<i>Tropidurus torquatus</i>	1	0	0	1	4
<i>Uranoscodon superciliosa</i>	1	2	1	1	1
<i>Mabuya mabouya</i>	3	4	4	3	2
<i>Alopoglossus carinicaudatus</i>	0	1	0	0	0
<i>Ameiva ameiva</i>	1	0	0	3	4
<i>Arthrosaura kochii</i>	1	0	0	0	0
<i>Cnemidophorus lemniscatus</i>	0	0	0	0	3
<i>Crocodylus lacertina</i>	0	1	0	0	0
<i>Dracaena guianensis</i>	0	0	0	0	1
<i>Kentropyx calcaratus</i>	4	4	4	2	0
<i>Leposoma percarinatum</i>	0	2	0	0	1
<i>Prionodactylus argulus</i>	1	2	0	0	0
<i>Tupinambus nigropunctatus</i>	1	1	0	1	2

altamazonica, is abundant in capoeira, terra firme, and varzea areas, but few individuals are found in the terra firme-varzea transition area. *Leptodactylus marmoratus* occurs predominantly in well-drained areas, but *Gonatodes humeralis* tolerates wet and dry areas.

RESOURCE PARTITIONING

Extensive field observations were carried out in an effort to discern whether species do indeed partition environmental resources. Resources examined were those aspects of the habitat which are important to the daily and seasonal activities of the species as follows: frogs—standing bodies of water, calling sites, and vegetation and ground area used for daily activities; salamanders—vegetation used for nocturnal activities; lizards—vegetation and ground area used for basking sites and other diurnal activities.

For purposes of analysis, the environment can be divided into vertical and horizontal components such as arboreal (high and low), terrestrial, aquatic margin, and aquatic. The distribution of species in these subdivisions of each of the five major areas is shown in table 3. Most species studied are either low arboreal or terrestrial.

TABLE 3.—Distribution of Species of Frogs and Lizards Within Subdivisions of Five of the Major Areas. Numbers preceding hyphens are frogs, and numbers following hyphens are lizards.

Subdivision	Terra Firme	Varzea	Igapó	Capoeira	Open & Edge
Arboreal (high)	0-3	1-3	0-1	0-2	1-1
Arboreal (low)	9-6	11-6	9-5	4-4	16-2
Terrestrial	9-6	7-5	3-2	4-5	4-7
Aquatic Margin	1-0	2-0	1-0	0-0	3-0
Aquatic	0-0	1-1	0-0	0-0	0-0

Spatial overlap among some species does exist. Salamanders and *Hyla* sp. (*rubra*-like) overlap greatly in their utilization of low vegetation in terra firme and varzea areas at night, presumably for obtaining food; also present, sharing the same vertical component, are numerous sleeping lizards (*Gonatodes humeralis*). Although these three species are the most abundant vertebrates using this aspect of the environment at night, the population densities appear to be so low that it is unlikely that significant interspecific competition exists.

There is evidence of breeding site partitioning in frogs, probably indicative of differing requirements of various species. Some tree frogs, such as *Hyla baumgardneri*, *H. egleri*, and *H. goughi* breed in diverse types of ponds and swamps, large or small, deep or shallow; apparently the frogs require only standing water and emergent vegetation. On the other hand, *Hyla minuta*, *H. raniceps*, and *Phyllomedusa hypochondrialis* are found in only some of the same areas as *H. baumgardneri*, *egleri*, and *goughi*. *Hyla raniceps* breeds only in larger bodies of water, at least 8 m by 15 m, usually at least 0.6 m in depth. *Phyllomedusa hypochondrialis* is restricted to ponds bordered by dense vegetation. The distribution of *H. minuta* is more difficult to interpret; the frogs occur in all types of areas, but without any regular pattern. For instance, numerous males call from one pond and not from a nearby pond having similar size, water depth, and emergent vegetation. The population density of this species appears to be lower than those of *H. baumgardneri*, *H. egleri*, and *H. goughi*. Perhaps male *H. minuta* attract other males to an area for the purpose of forming breeding congregations. This formation would be of greater importance to a less abundant species than to a more common one and would explain the fact that usually these frogs call in groups of at least 15 individuals in contrast to *H. baumgardneri*, *H. egleri*, and *H. goughi* which often call in groups of 10 or less.

Many species of frogs which breed sympatrically demonstrate calling site segregation (Tables 4 and 5). Most species characteristically call from a certain physiognomic type of vegetation, at a relatively uniform height from the water. The type of vegetation utilized is correlated with the body build and size of the animal. Large, heavy frogs generally call from the ground, sturdy vegetation near the ground, or from branches of trees; small frogs usually call from grass stems or leaves and small branches from emergent and edge vegetation. Some species have a broader range of calling sites than do others. For example, *Hyla goughi* commonly calls from both emergent and edge vegetation, 0.05-1.5 m above the water,

TABLE 4.—Species of Frogs Breeding and/or Calling at Least Partially Sympatrically and Synchronously.

Species	Calling Site	Jan.	Feb.	Mar.	Apr.	May	June	July
<i>Bufo marinus</i>	ground	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>Physalaemus ephippifer</i>	ground	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>Leptodactylus ocellatus</i>	ground	-----	-----	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>Hyla rubra</i>	ground & low vegetation	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>Hyla</i> sp. (<i>large rubra</i>)	ground & low vegetation	-----	-----	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>Hyla multifasciata</i>	ground & low vegetation	-----	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>Hyla baumgardneri</i>	low vegetation	-----	-----	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>Hyla boesemani</i>	low vegetation	-----	-----	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>Hyla eglei</i>	low vegetation	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>Hyla gongchi</i>	low vegetation	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>Hyla minuta</i>	low vegetation	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>Hyla nana</i>	low vegetation	-----	-----	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>Hyla leucophyllata</i>	low vegetation	XXXXXX	-----	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX

whereas *Phyllomedusa hypochondrialis* always calls from edge vegetation usually 0.6-1.5 m above the ground or water. Complete segregation of calling sites does not exist for all species in all areas. Segregation is partially dependent on species composition at the site, relative abundance of the calling individuals, and on the size of the breeding site relative to the population densities. Generally, in large, mixed congregations segregation tends to break down, and the frogs call from whatever sites are available. Interspecific competition for calling sites is probably significant during times of much reproductive activity. Segregation is more pronounced in large areas with distinct physiognomic vegetational diversity than in smaller areas with less calling site diversity. A commonly accepted explanation for the evolution of partitioning of calling sites is the resultant tendency to reduce the chances of interspecific mating. However, because segregation breaks down in large, mixed congregations at the time it is most needed, I propose that calling site partitioning exists due to the structural and behavioral attributes of each species rather than as a necessary reproductive isolating mechanism; advantages likely include improved mating efficiency and reduced energy expenditure.

There is a definite replacement of several species of tree frogs at breeding sites because of calling site overlap. *Hyla boesemani*, *H. multifasciata*, *H. raniceps*, and *H. rubra* all call from thick clumps of emergent vegetation, usually within 20 cm of the water. Individuals of all four species call from the same swampy areas, but not all at the same time; the only two of these species ever found calling sympatrically and synchronically are *H. boesemani* and *H. rubra*, the two smaller species. Every congregation of *Hyla* sp. (large *rubra*) observed was found calling in association with *H. rubra*. Male *Hyla* sp. (large *rubra*) call from the ground or low, thick vegetation. They seem to be dominant over *H. rubra* as indicated by calling site displacement of *H. rubra* when the two species call sympatrically. *Hyla rubra* usually calls from low vegetation, but when *Hyla* sp. (large *rubra*) is also calling from the area, the former calls from higher vegetation.

Perhaps some syntopic species (species with similar habitats) coexist with minimum interspecific competition as a result of temporal partitioning of the environment, in terms of diel and seasonal activities. For example, the nocturnal gecko, *Thecadactylus rapicaudus*, is likely the temporal replacement for diurnal lizards feeding on similar species of insects and utilizing the same habitat. The two species of dendrobatid frogs use the same forest floor by day that several species of leptodactylids utilize at night. Frogs demon-

TABLE 5.—Partitioning of Calling Sites of Species of Frogs.

Species	VARZEA			IGAPÓ			OPEN & EDGE		
	High	Low	Ground	High	Low	Ground	High	Low	Ground
<i>Leptodactylus marmoratus</i>	—	—	X	—	—	—	—	—	—
<i>Leptodactylus ocellatus</i>	—	—	—	—	—	—	—	—	X
<i>Leptodactylus wagneri</i>	—	—	X	—	—	X	—	—	—
<i>Physalaemus ephippifer</i>	—	—	X	—	—	—	—	—	X
<i>Physalaemus petersi</i>	—	—	X	—	—	—	—	—	X
<i>Bufo marinus</i>	—	—	—	—	—	—	—	—	X
<i>Hyla baumgardneri</i>	—	—	—	—	X	—	—	X	—
<i>Hyla boesemani</i>	—	—	—	—	—	—	—	X	—
<i>Hyla calcarata</i>	—	—	—	—	—	—	—	—	—
<i>Hyla egleri</i>	—	X	—	—	—	—	—	—	—
<i>Hyla geographica</i>	—	X	—	—	X	—	—	—	—
<i>Hyla gonghi</i>	—	X	X	—	—	—	—	—	—
<i>Hyla granulosa</i>	—	X	—	—	—	—	—	—	—
<i>Hyla leucophayllata</i>	—	X	—	—	X	—	—	—	—
<i>Hyla melanargyrea</i>	—	—	—	—	—	—	—	X	—
<i>Hyla minuta</i>	—	—	—	—	—	—	—	X	—
<i>Hyla multifasciata</i>	—	—	—	—	—	—	—	X	—
<i>Hyla nana</i>	—	X	—	—	—	—	—	X	—
<i>Hyla rubra</i>	—	X	—	—	—	—	—	X	—
<i>Hyla</i> sp. (large <i>rubra</i>)	—	—	—	—	X	—	—	X	X
<i>Phyllomedusa bicolor</i>	X	—	—	—	—	—	X	—	—
<i>Phyllomedusa hypochondrialis</i>	—	—	—	—	—	—	—	—	—
<i>Sphaenorhynchus euryostus</i>	—	X	—	—	—	—	—	X	—

strate seasonal partitioning of the environment in terms of breeding activities (Table 6). *Hyla multifasciata* and *H. raniceps* both call from low vegetation in swampy, open areas; they are rather large tree frogs with similar mating calls. The former is a wet season breeder, whereas the latter is a dry season breeder. Most of the frogs are nocturnal (83.8%) and most of the lizards are diurnal (91.7%); the salamander is nocturnal. In the terra firme and varzea forests, 50 percent of the frogs, salamanders, and lizards considered as a group are diurnal; the distribution in the igapó forest is similar, with 45.5 percent diurnal and 54.5 percent nocturnal. Most of the species in open and edge areas are nocturnal (73.5%); breeding tree frogs account for most of this distribution. On the other hand, most of the species in the capoeira area are diurnal (70%); over half of these species are lizards, many of which are heliotherms (Table 7).

CONTINGENCY TABLE ANALYSIS

The contingency table analysis technique, developed by Williams (1952) as an extension of Fisher and Yates' ideas for dealing with frequency counts in two-way tables, is employed here for two reasons: 1) to measure the degree of association between species and plots; and 2) to partition the species-plot association into independent components representative of environmental gradients. The analysis was carried out on 20 species of frogs, salamanders, and lizards from 44 sampling plots, each 20×30 m, from the capoeira-terra firme transition, terra firme-varzea transition, varzea, and igapó areas. All plots received approximately equal amounts of sampling time from mid-January to the end of July. The 20 species were the only species of frogs, salamanders, and lizards found within the boundaries of the particular plots analyzed. The total sample includes 1218 individuals (Table 8). Most individuals were not removed from the habitat, so the relative abundance indices are possibly inclusive of re-counted individuals; each observation was treated as a unit indicative of species-habitat association.

TABLE 7.—Comparison of Activity Cycles of Amphibians and Lizards in Five of the Major Areas. Absolute number of species and percentage of species within each area are given.

Period of Activity	Terra Firme	Varzea	Igapó	Capoeira	Open & Edge
Diurnal	18 50%	19 50%	10 45.5%	14 70%	9 26.5%
Nocturnal	18 50%	19 50%	12 54.5%	6 30%	25 73.5%

TABLE 8.—Summary of the Species \times Plot Data Matrix used for Contingency Table Analysis.

Species	N	Capoeira-Terra Firme Transition (4 plots)	Terra Firme-Varzea Transition (19 plots)	Varzea (9 plots)	Igapó (12 plots)
<i>Bufo typhlopinus</i>	123	21	102	—	—
<i>Dendrobates ventrimaculatus</i>	10	—	—	2	8
<i>Hyla baumgardneri</i>	12	—	—	—	12
<i>Hyla eglei</i>	11	—	2	—	9
<i>Hyla geographica</i>	23	—	2	21	—
<i>Hyla granulosa</i>	14	—	—	1	13
<i>Hyla rubra</i>	36	5	—	22	9
<i>Hyla</i> sp. (rubra-like)	60	34	—	26	—
<i>Leptodactylus marmoratus</i>	190	19	171	—	—
<i>Leptodactylus wagneri</i>	112	—	24	33	55
<i>Physalaemus ephippifer</i>	21	—	21	—	—
<i>Physalaemus petersi</i>	18	—	17	1	—
<i>Bolitoglossa altamazonica</i>	36	21	—	15	—
<i>Anolis fuscovaratus</i>	22	8	3	11	—
<i>Gonatodes humeralis</i>	313	38	158	88	29
<i>Kentropyx calcaratus</i>	142	8	16	36	82
<i>Leposoma petersianum</i>	4	—	2	2	—
<i>Mabuya mabouya</i>	54	5	4	10	35
<i>Plica mibra</i>	14	9	4	—	1
<i>Uranoscodon superciliosus</i>	3	—	—	3	—
Total No. Individuals	1218	168	526	271	253
Total No. Species	20	10	13	14	10

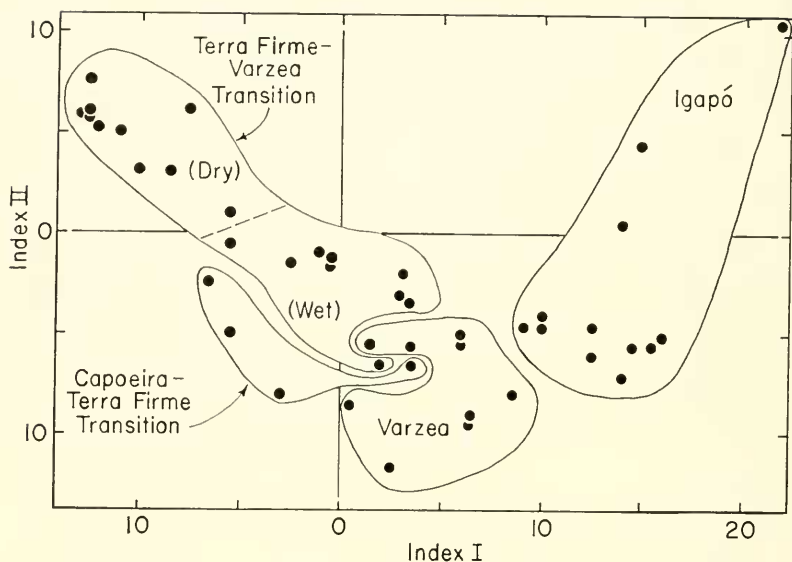


FIG. 12. Scores on index I plotted against scores on index II for each of 44 plots. Each dot represents the position of a particular plot relative to the x and y axes. Index I is a moisture gradient from dry (negative) to wet (positive). Index II is a vegetation density gradient from dense ground cover (negative) to grassy ground cover (positive).

The data were assembled into a species \times plot table; the species frequency counts represent the number of individuals of each species which occurred in a particular plot. Williams (1952) showed that when actual environmental measurements were unavailable, scores could be calculated from the data of the contingency table by simply using those sets of scores for which there is maximum correlation. The interpretation is feasible because the scores are adjusted to have a mean of zero and a variance of one.

The computer print-out for the analysis consists of a series of indices, each representing an environmental gradient or a composite of such gradients. Each index maximizes the measure of association between the two sets of variables—species and plots. Index scores relative abundances are presented in table 9. The results are presented by Cartesian (x, y) scattergrams of two sets of scores (Figs. 12-17). In this way, two gradients (two indices) can be studied simultaneously and their interaction examined. Species or plots having similar index scores appear close together on the diagram. Thus, ecologically similar plots and species with similar distributions can be identified.

No actual environmental measurements were taken; resource

TABLE 9.—Tabulation of Relative Abundance, Contingency Table Indices, and Niche Breadth Scores. Numbers are the results from analytical techniques applied to a species \times plot data matrix, dimensions 20×44 , summarized in Table 8.

Species	Series Number	Relative Abundance					Contingency Table Indices					Niche Breadth
		Relative Abundance					Contingency Table Indices					
		Capoeira-Terra Firme Transition	Terra Firme-Varzea Transition	Varzea	Igapo	Accumulative Relative Abundance (× 1000)	I	II	III	IV		
<i>Bufo typhonius</i>	1	0.01724	0.08375	-----	-----	101	-12.37	5.20	-0.71	3.94	9.31	
<i>Dendrobates ventrimaculatus</i>	2	-----	-----	0.00164	0.00657	8	17.64	-0.79	-2.00	19.24	5.00	
<i>Hyla baumgardneri</i>	3	-----	-----	-----	0.00985	10	28.11	61.66	21.96	-17.35	1.00	
<i>Hyla eglei</i>	4	-----	0.00164	-----	0.00739	9	20.71	52.27	17.26	-12.99	1.46	
<i>Hyla geographica</i>	5	-----	0.00164	0.01725	-----	19	6.65	-11.58	-4.05	-25.88	4.30	
<i>Hyla granosa</i>	6	-----	-----	0.00082	0.01067	11	21.15	23.56	2.95	0.23	3.27	
<i>Hyla rubra</i>	7	0.00411	-----	0.01806	0.00739	30	9.77	-9.55	12.71	22.48	5.31	
<i>Hyla sp. (rubra-like)</i>	8	0.02792	-----	0.02134	-----	49	-0.77	-11.79	25.47	-15.48	4.46	
<i>Leptodactylus marmoratus</i>	9	0.01560	0.14040	0.02709	0.04515	156	-12.97	6.32	-2.56	4.11	10.76	
<i>Leptodactylus wagneri</i>	10	-----	0.01971	-----	-----	92	10.92	-5.09	-14.36	-7.04	11.86	
<i>Physalaemus ephippifer</i>	11	-----	0.01724	-----	-----	17	-2.35	-2.59	-21.69	-38.69	6.78	
<i>Physalaemus petersi</i>	12	-----	0.01396	0.00082	-----	15	-8.62	4.06	-10.81	-6.31	6.48	
<i>Bolitoglossa altamazonica</i>	13	0.01724	-----	0.01232	-----	30	0.11	-11.59	25.01	-6.96	5.59	
<i>Anolis fuscoauratus</i>	14	0.00656	0.00246	0.00903	-----	18	-0.41	-7.63	13.41	7.31	8.34	
<i>Gonatodes humeralis</i>	15	0.03120	0.12972	0.07224	0.02381	257	-2.43	-1.25	-0.66	-1.45	32.01	
<i>Kentropyx calcaratus</i>	16	0.00657	0.01313	0.02955	0.06732	117	10.99	-3.77	-4.39	9.44	21.68	
<i>Leposoma percarinatum</i>	17	-----	0.00164	0.00164	-----	3	1.09	-3.87	-6.73	-9.25	4.00	
<i>Mabuya mabouya</i>	18	0.00410	0.00328	0.00822	0.02874	44	12.84	0.31	-0.65	9.66	16.38	
<i>Plica umbra</i>	19	0.00738	0.00328	-----	0.00082	11	-3.13	-4.62	9.63	0.96	5.44	
<i>Uranoscodon superciliosa</i>	20	-----	-----	0.00246	-----	2	6.91	-11.57	8.64	7.91	3.00	

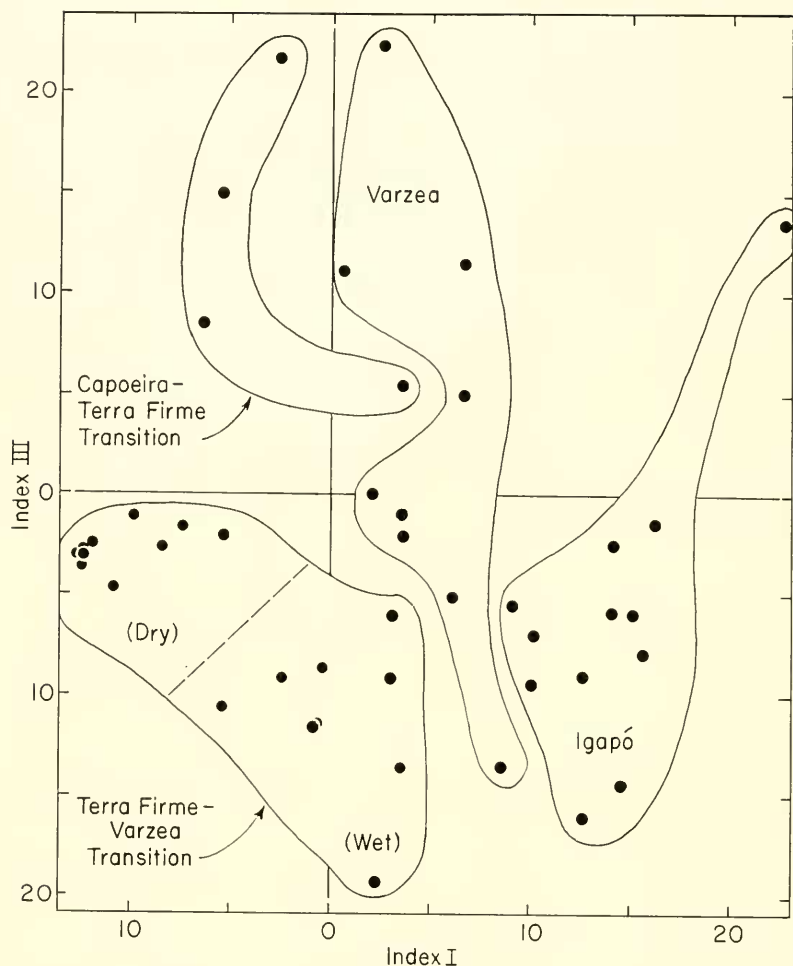


FIG. 13. Scores on index I plotted against scores on index III for each of 44 plots. Each dot represents the position of a particular plot relative to the x and y axes. Index I is a moisture gradient from dry (negative) to wet (positive). Index III is the vertical distribution of species found within the plots from terrestrial (negative) to low vegetation (positive).

requirements for each species were analyzed indirectly by assuming that a given sampling plot provides necessary resources for the species found therein. For this reason interpretation of the indices is inferential.

Environmental gradients.—The first four index scores from the contingency table analysis were analyzed in an attempt to: 1) determine the major limiting environmental parameters affecting the

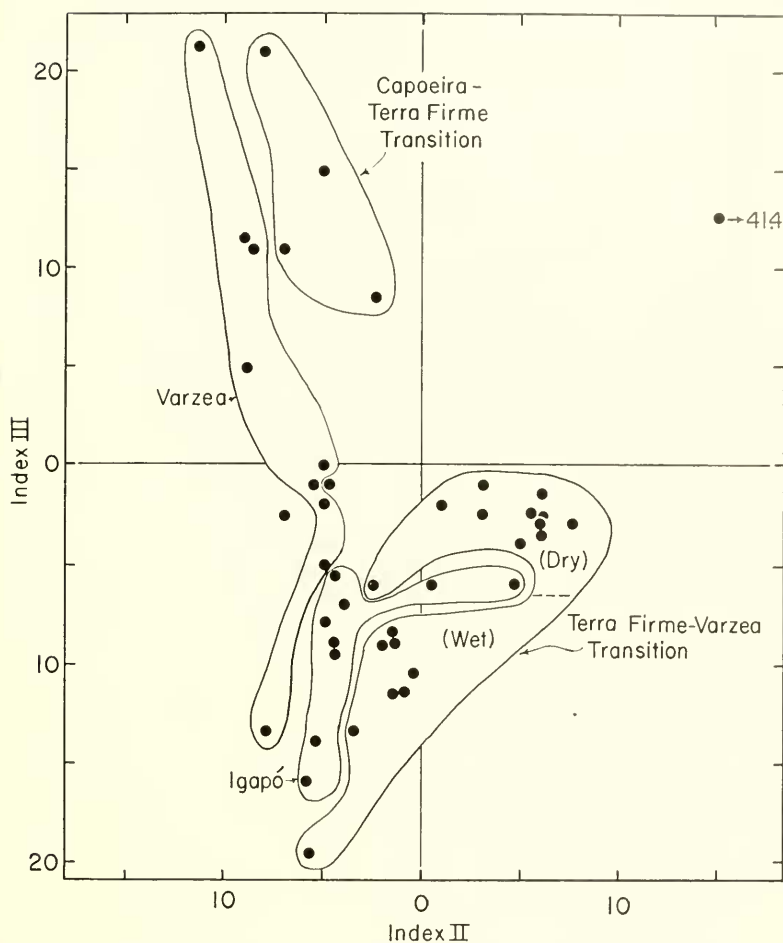


FIG. 14. Scores on index II plotted against scores on index III for each of 44 plots. See figures 12 and 13 for explanation of dots and indices. The three dots not included within forest boundaries all are igapó plots.

distribution of species; 2) characterize the four major forest areas in terms of those limiting factors relevant to frogs, salamanders, and lizards; and 3) identify the habitat of each of the 20 species in terms of the environmental parameters represented by the indices.

The first index indicates a moisture gradient from dry (low values) to wet (high values). Moisture probably is the most critical factor affecting the ecological distribution of amphibians and reptiles in the study area.

Probably the next most critical limiting factor is the physiognomy of the vegetation. The second index is indicative of vegetation

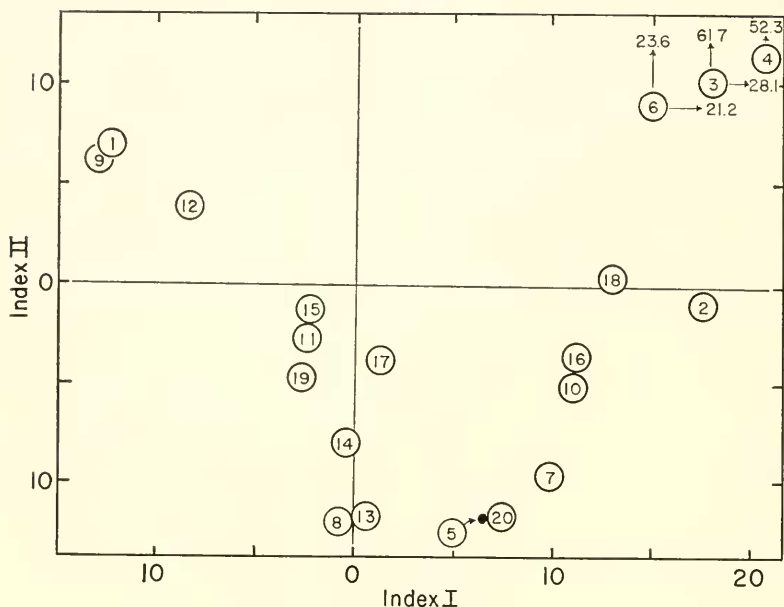


FIG. 15. Scores on index I plotted against scores on index II for each of 20 species. See figure 12 for explanation of the indices. Each circle represents the position of a particular species relative to the x and y axes. The species numbers are associated with species names in table 9, p. 29.

ground cover. The spectrum is from dense ground cover (low values) to grassy areas (high values). The second index may also indicate light intensity, resulting from the structure and density of the vegetation. In general, areas with dense ground cover are darker habitats than are grassy open areas.

The third index probably is a combination of factors affecting vertical distribution. Terrestrial species have low values, and species which inhabit low vegetation have high values. Lizards found on tree trunks and along the boardwalks have intermediate scores.

The fourth index seems to be a composite of many factors. Some of the following may be involved, but no one of them is responsible for the separation of the plot or species scores: 1) temporal activity (diel and seasonal); 2) organism size; 3) phylogenetic position of organisms; 4) heliophilous versus sciophilous organisms; 5) niche breadth of organisms; 6) abundance of animals within plots; and 7) solitary organisms versus congregations. The fourth index segregates the following species pairs, which are similar on the basis of the first three indices: *Hyla rubra* and *Hyla* sp. (*rubra*-like), *Hyla geographica* and *Uranoscodon superciliosa*, and *Hyla rubra* and *Bolitoglossa altamazonica*.

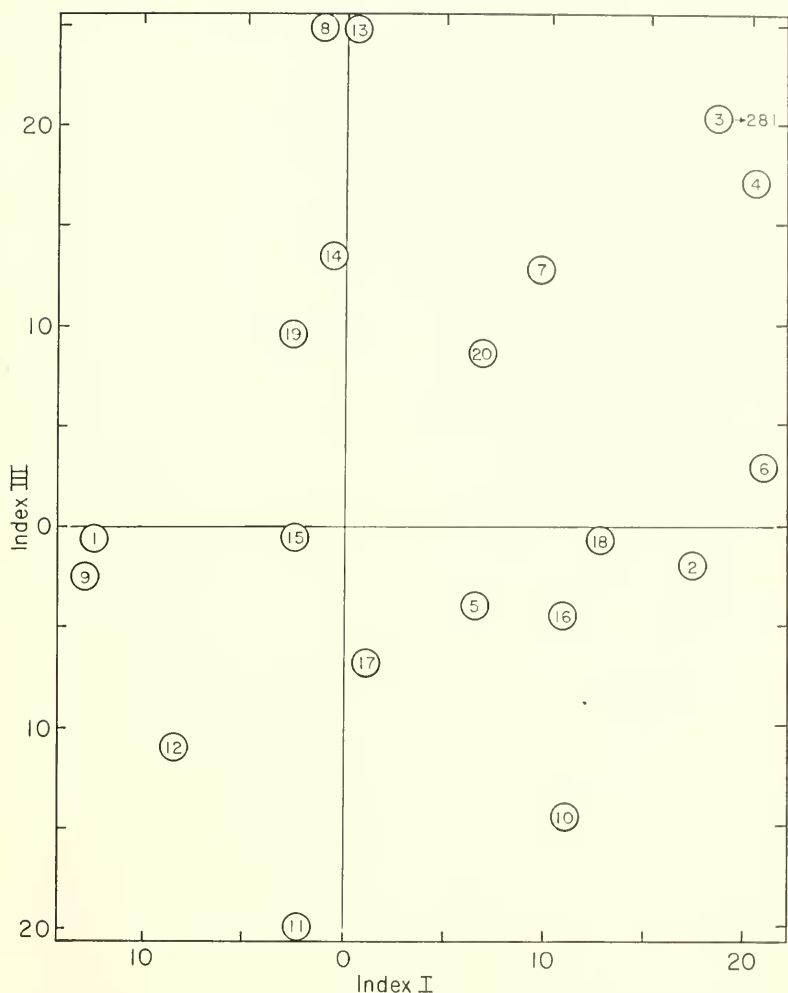


FIG. 16. Scores on index I plotted against scores on index III for each of 20 species. See figures 13 and 15 for explanation of indices and circles/species numbers respectively.

When the scores of the first three indices for the 44 plots (Table 10) are plotted against each other, it is possible to characterize the four major areas in terms of the environmental gradients analyzed (Figs. 12-14). Likewise, when the species scores are plotted, it is possible to get some understanding of the habitat of each species in terms of the environmental gradients inferred from the indices (Figs. 15-17).

Plot index scores.—Four capoeira-terra firme transition plots

TABLE 10.—Contingency table indices for each of 44 plots analyzed. Plot numbers are located on figures 10 and 11. Indices are plotted on figures 12-14.

Plot No.	Index I	Index II	Index III
1	3.66	-6.77	10.62
4	-3.13	-7.83	20.81
11	-6.50	-2.36	8.60
12	-5.57	-4.80	14.94
15	-5.74	0.88	-1.96
16	-0.67	-1.32	-8.52
17	-8.55	2.79	-2.38
18	-7.60	6.06	-1.55
19	-10.78	4.77	-4.29
20	-12.62	5.93	-2.88
22	-12.39	6.03	-3.31
23	-10.17	3.26	-1.02
24	-12.35	7.34	-3.19
25	-1.16	-0.88	-11.55
26	3.26	-3.47	-13.31
27	-2.30	-1.51	-9.13
28	1.87	-6.29	-25.82
29	-5.26	-0.48	-10.31
30	3.02	-1.95	-8.83
31	-0.67	-1.45	-11.32
33	2.82	-2.87	-6.13
42	-12.05	5.54	-2.63
43	-12.58	6.11	-2.95
44	6.64	-9.18	5.09
45	0.55	-8.65	10.87
46	2.34	-11.48	22.55
49	5.89	-5.08	-4.86
50	1.74	-5.26	-0.18
51	8.56	-8.12	-13.45
52	6.33	-8.77	11.53
53	3.38	-4.85	1.81
54	3.44	-5.34	-0.96
65	22.25	41.36	13.27
66	14.31	-5.39	-14.28
67	15.00	4.45	-5.85
68	13.83	0.45	-5.74
69	13.92	-6.85	-2.69
70	15.77	-4.80	-1.69
71	12.38	-4.32	-8.75
72	15.28	-5.04	-7.98
73	9.76	-4.10	-7.00
74	8.98	-4.33	-5.59
75	9.82	-4.66	-9.33
76	12.64	-5.78	-15.93

were studied. In general, these plots are characterized by low to mid-range values on the first index, fairly low on the second, and high on the third (Figs. 12-14). The area is towards the drier end of the moisture spectrum and near the denser end of the vegetation



FIG. 17. Scores on index II plotted against scores on index III for each of 20 species. See figures 12 and 13 for an explanation of indices and figure 15 for an explanation of circles.

density spectrum. The value on the third index suggests that the herpetofauna of this area is predominantly found on low vegetation rather than on the ground.

Nineteen plots are terra firme-varzea transition areas, and can be divided into two groups, dry transition and wet transition (Fig. 10). The two transition areas are clearly segregated when the index values are plotted against each other (Figs. 12-14). The entire transition zone is characterized by low to mid-range values on the

first index, high on the second, and low to middle on the third. The area represents an intermediate zone with regard to the physical environmental parameters, except on the second index, indicating that the ground cover is relatively grassy. One plot is extremely low on the third and fourth indices and segregates from the other transition plots. The low value on the third index is explained by the many terrestrial leptodactylids found calling from temporary puddles.

Nine varzea plots were analyzed (Fig. 11). There is a very small range of variation on the first and second indices, but a wide range on the third and fourth. In general, most plots have a fairly high value on the first index, low on the second, and from low to high on the third. The varzea is a wet environment with relatively dense ground cover; the organisms are neither predominantly terrestrial nor inhabitants of low vegetation.

Twelve igapó plots were studied. These plots have the highest values on the first index, indicating that the igapó is the wettest area. Most values on the second index range from low to middle and most on the third are low. The igapó forest has a relatively dense to intermediate vegetation ground cover. Most of the lizards are terrestrial or are found predominantly on the boardwalks. When the indices are plotted against each other, one plot is segregated from the other igapó plots by high values on the second and third indices (Figs. 12-14). The second index score is explained by the presence of large clumps of tall emergent grass in the plot. Two species of tree frogs not found elsewhere in the igapó forest utilize the grass for calling sites; this creates a higher third index score than those values for igapó plots in which there are many terrestrial lizards.

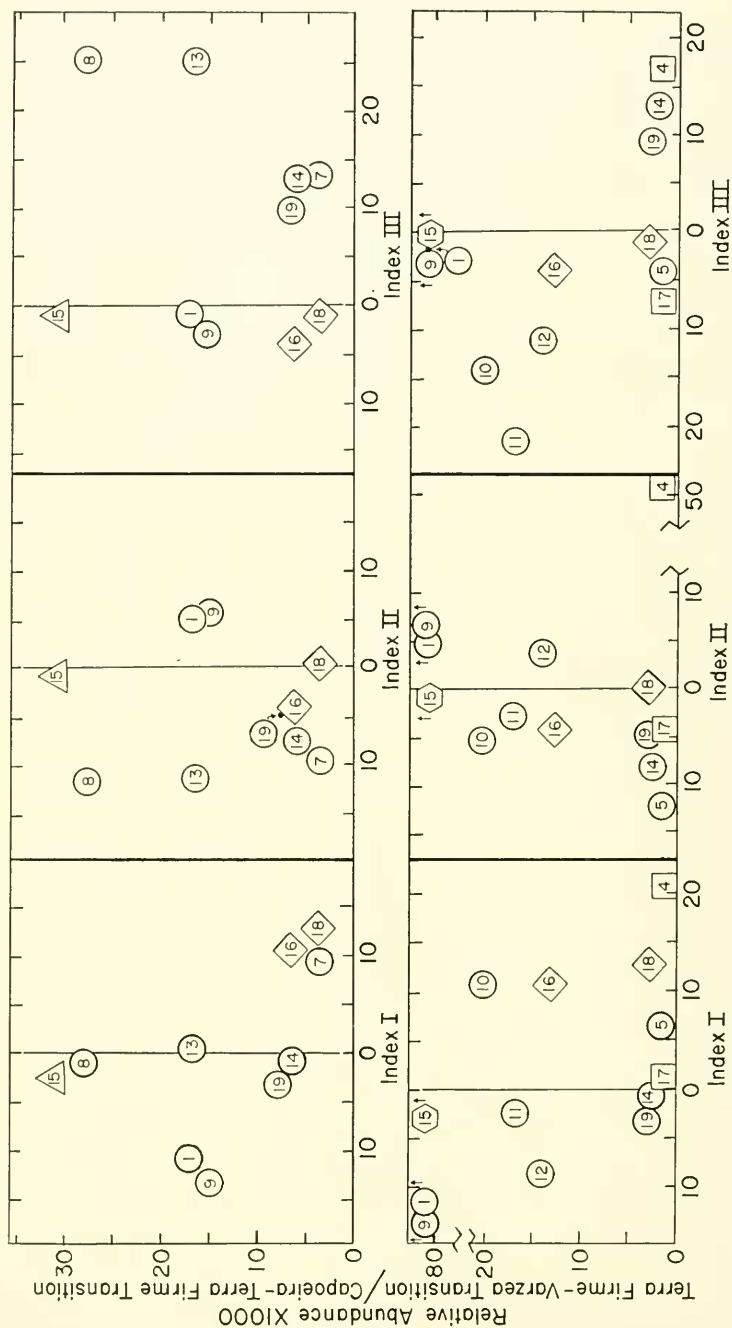
Species index scores.—The Cartesian plots of index values (Figs. 18-21) and the bar diagrams (Figs. 22-24) illustrate that each species has requirements and tolerances with regard to the environmental gradients. Several trends represented by correlations between species abundances and availability of a particular resource are evident (Figs. 22-24). For example, index I represents a moisture gradient; those species with the highest positive values are those found in association with wet areas. Each of the seven species with the highest scores (*Leptodactylus wagneri*, *Kentropyx calcareatus*, *Mabuya mabouya*, *Dendrobates ventrimaculatus*, *Hyla egleri*, *H. granosa*, and *H. baumgardneri*) is most abundant in the igapó forest, less abundant in the varzea forest, still less common in the terra firme-varzea transition area, and rare in the capoeira-terra firme transition area, if found in the last two areas at all. The two species with extremely low negative scores on the first index (*Lepto-*

dactylus marmoratus and *Bufo typhonius*) are more abundant in the terra firme-varzea transition area than in capoeira-terra firme transition plots, contrary to what one might expect. The distribution is better understood when the second index scores are considered; both species have positive scores, but neither one is extreme. Apparently these terrestrial species inhabit relatively dry areas but avoid the open areas characteristic of capoeira forest in preference to the denser undergrowth of high ground, dry terra firme-varzea transition areas.

In most instances, those species with scores closest to zero are the most abundant. This is probably because those species requiring neither extreme (considered generalized) are able to utilize more of the environment. If more of the environment is potentially available for exploitation by a species, it can be assumed that the potential carrying capacity of the environment for that species is greater than that for a specialized species restricted to a particular habitat. *Gonatodes humeralis* is the most abundant of the twenty species and has scores near zero on each of the four indices. The three next most abundant species, *Leptodactylus marmoratus*, *Kentropyx calcaratus*, and *Bufo typhonius*, have scores relatively close to zero on all indices except the first. Species with extremely high positive or low negative scores on index IV are relatively uncommon.

Most species of lizards do not have extreme values on any of the environmental gradients. *Gonatodes humeralis*, *Kentropyx calcaratus*, and *Mabuya mabouya* are the only species found in all four major areas; none has extreme index values. The combined cumulative relative abundances (the three species from the four areas) represents 509 individuals, or 41.8 percent of the total sampled herpetofauna. *Gonatodes humeralis* is less abundant in the igapó forest than in the other three areas, whereas *K. calcaratus* and *M. mabouya* are most abundant in the igapó forest. The other four species of lizards are relatively uncommon in all of the areas. *Anolis fuscoauratus*, *Leposoma percarinatum*, and *Plica umbra* have no extreme index scores; the first two species are near zero on the moisture gradient, and *P. umbra* is near zero on the fourth index. *Uranoscodon superciliosa* is relatively generalized with respect to all the environmental gradients except vegetation density; the score on the second index is low, indicative of its occurrence in areas of dense vegetation.

In general, the amphibians demonstrate more extreme environmental requirements than do the lizards. None of the thirteen



FIGS. 18-19. Species scores on each of the three indices plotted against relative abundance $\times 1000$ in capoeira-terra firme (continued on next page)

species is found in all four areas. The salamander, *Bolitoglossa altamazonica*, has a score near zero on the moisture gradient, but exhibits extreme scores on the second and third indices, indicative of the occurrence of individuals on low vegetation in relatively dense areas. *Physalaemus petersi* is generalized with regard to all of the environmental gradients. *Bufo typhonius* and *Leptodactylus marmoratus* are specialized only with regard to the moisture gradient; they inhabit relatively dry areas. *Hyla granosa* is found in relatively open, very wet areas. This species is more abundant in the igapó forest than in the varzea forest; the fourth index score is almost zero. *Leptodactylus wagneri* is terrestrial, as indicated by the extremely low third index score; the species is more common in the varzea and igapo forests than in the terra firme-varzea transition area, apparently due to the absence of permanent standing water in the transition area. The fourth index yields extreme values for several of the species of frogs. *Physalaemus ephippifer*, *Hyla geographica*, *H. baumgardneri*, *Hyla* sp. (*rubra*-like), and *H. egleri* all have low scores; *Dendrobates ventrimaculatus* and *Hyla rubra* have high values. *Physalaemus ephippifer* is terrestrial, found only in the terra firme-varzea transition area. *Dendrobates ventrimaculatus* occurs in very wet areas of the varzea and igapo forests; the species is relatively uncommon in both areas. *Hyla geographica* and *H. rubra* are found in places of rather dense vegetation. The three most specialized species seem to be *Hyla baumgardneri*, *H. egleri*, and *Hyla* sp. (*rubra*-like). The first two species are found in very wet, open grassy areas, whereas *Hyla* sp. (*rubra*-like) is found in plots having intermediate values on the moisture gradient, with dense vegetation. All three species are found on low vegetation; all have extremely low values on the fourth index.

Of the twelve species of frogs, the only abundant ones are *Bufo typhonius*, *Leptodactylus marmoratus*, and *L. wagneri*, all of which are terrestrial, and mainly forest inhabitants. Three species of tree frogs, *Hyla baumgardneri*, *H. egleri*, and *H. rubra*, are found principally in open, non-forested areas, where they congregate at ponds and swamps to breed, thus explaining their relative uncommonness in the forest plots.

transition (figure 18, upper) and terra firme-varzea transition (figure 19, lower). See figures 12 and 13 for an explanation of indices. Species numbers are associated with species names in table 9, p. 29. Numbers enclosed in squares indicate species that are habitat specialists; circles are habitat intermediates; diamonds are relatively uncommon generalists; triangles are moderately common generalists, and hexagons are abundant generalists.

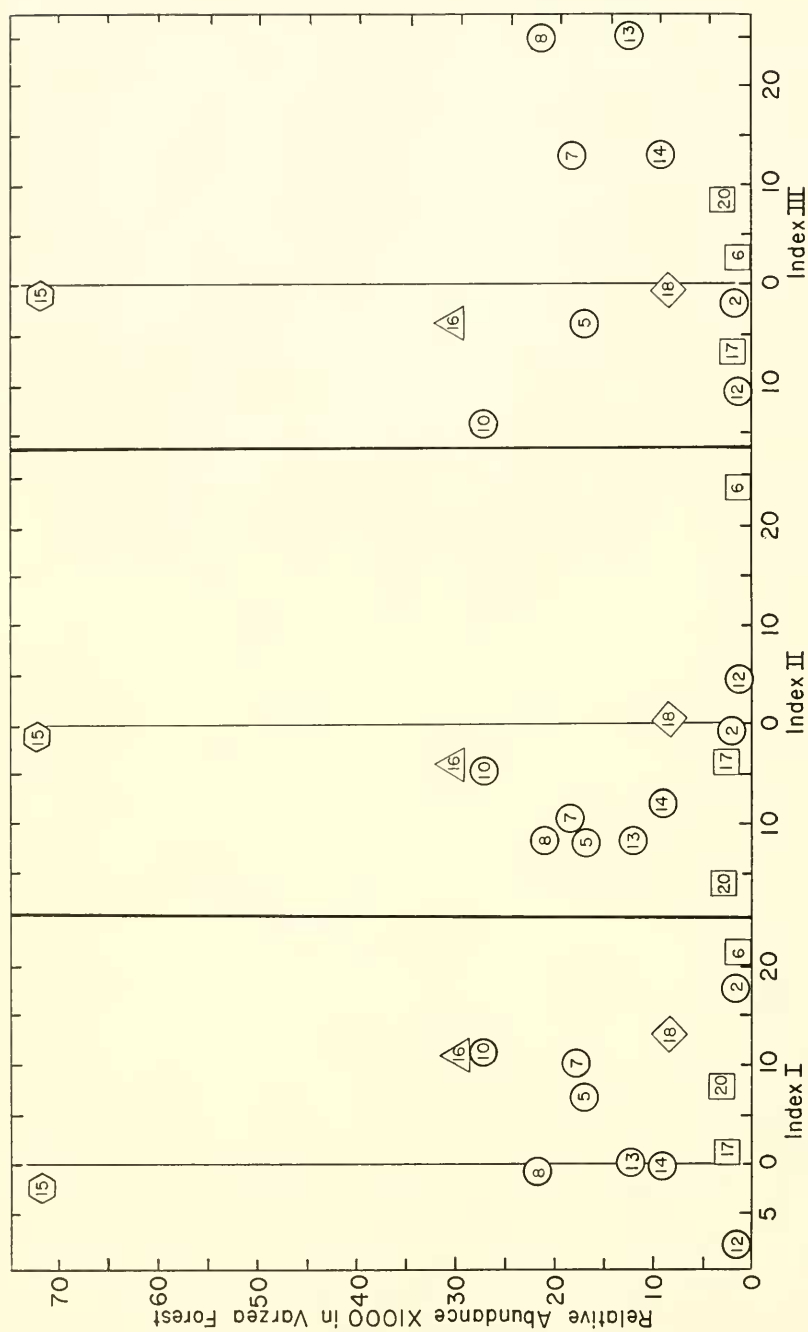


FIG. 20. Species scores on each of the three indices plotted against relative abundance $\times 1000$ in the varzea forest. Refer to figures 18 and 19 for explanation.

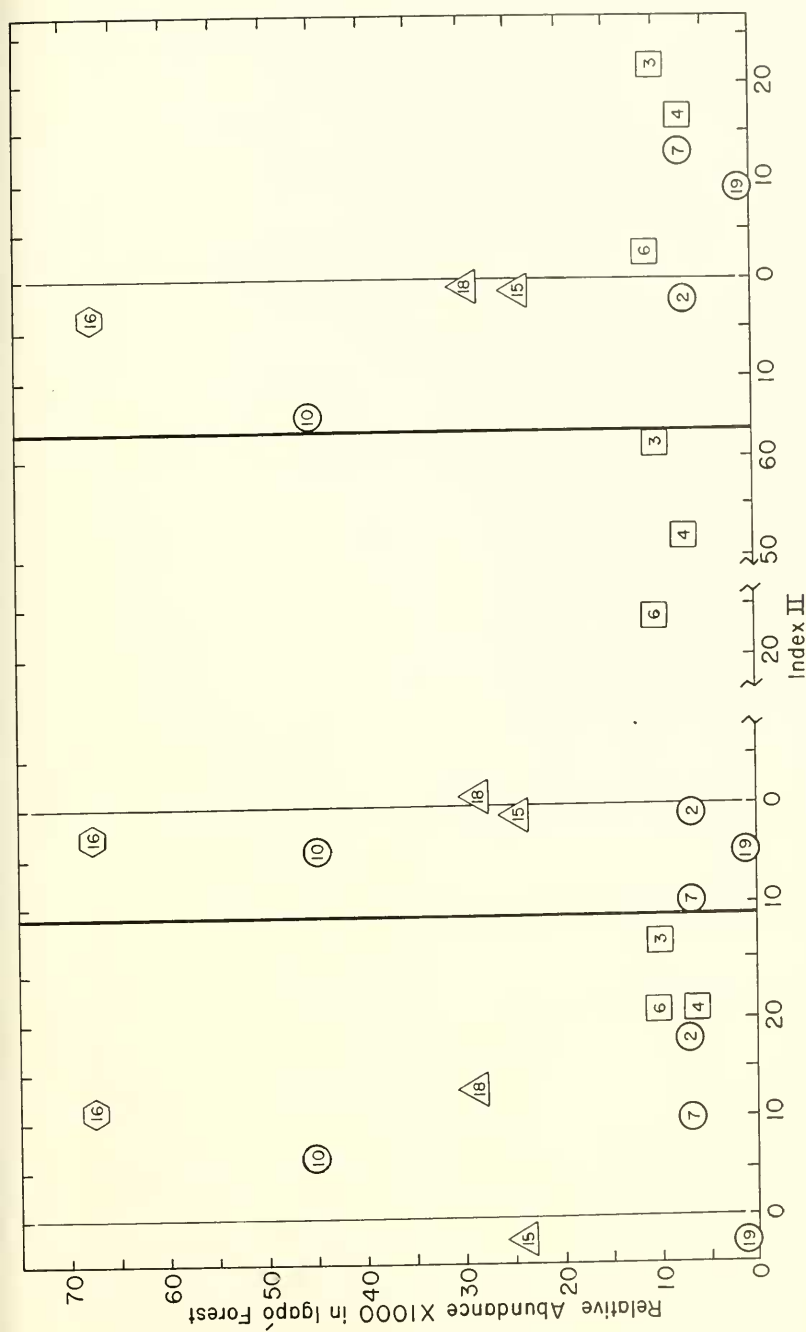


FIG. 21. Species scores on each of the three indices plotted against relative abundance $\times 1000$ in the igapó forest. Refer to figures 18 and 19 for explanation.

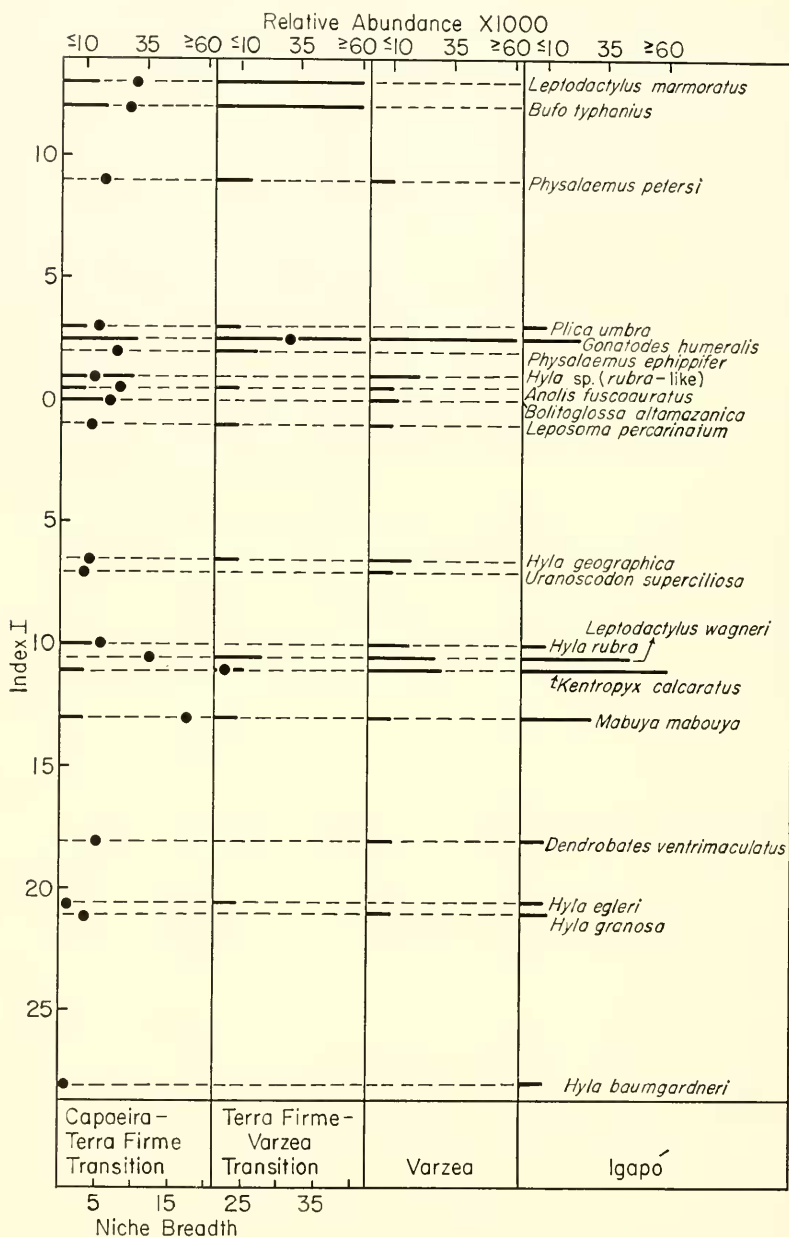


FIG. 22. Relationship of species scores on index I, relative abundance, and niche breadth scores for 20 species in each of the four major areas. Dots represent niche breadth scores. Horizontal bars indicate index scores and relative abundance.

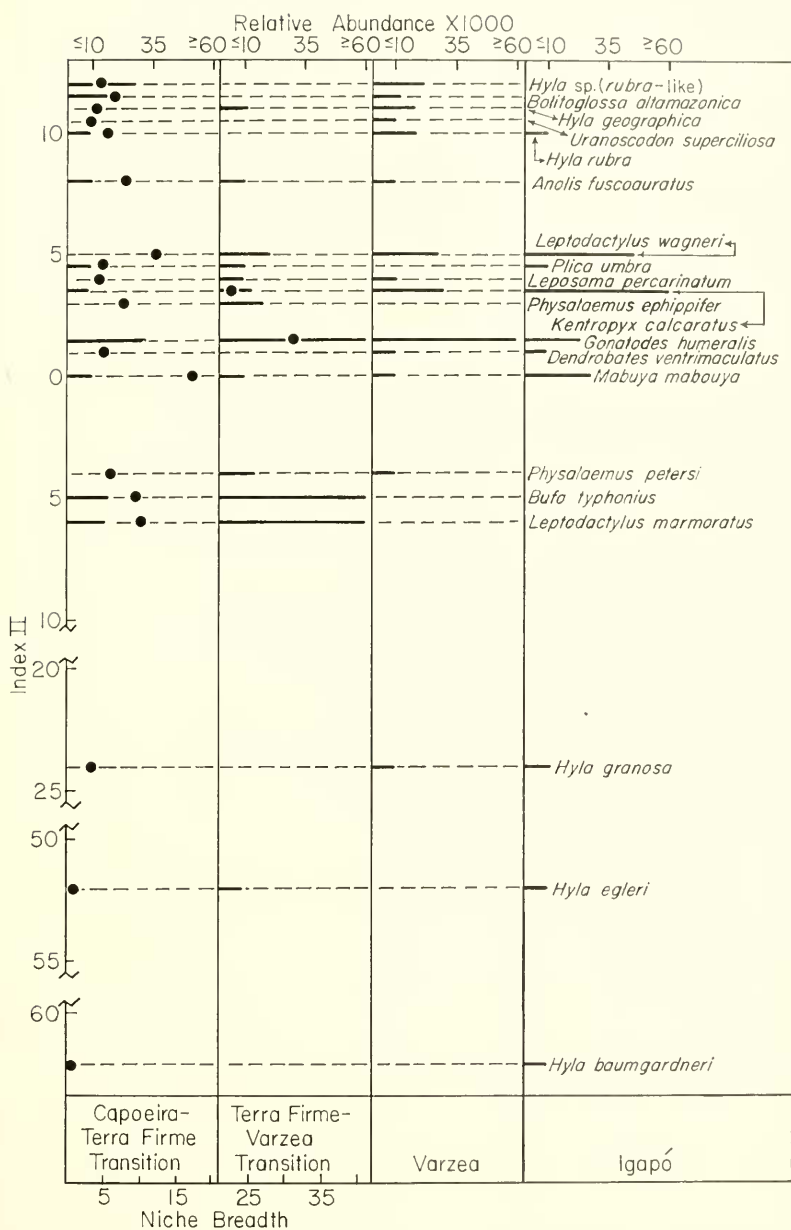


FIG. 23. Relationship of species scores on index II, relative abundance, and niche breadth scores for 20 species in each of the four major areas. See figure 22 for explanation.

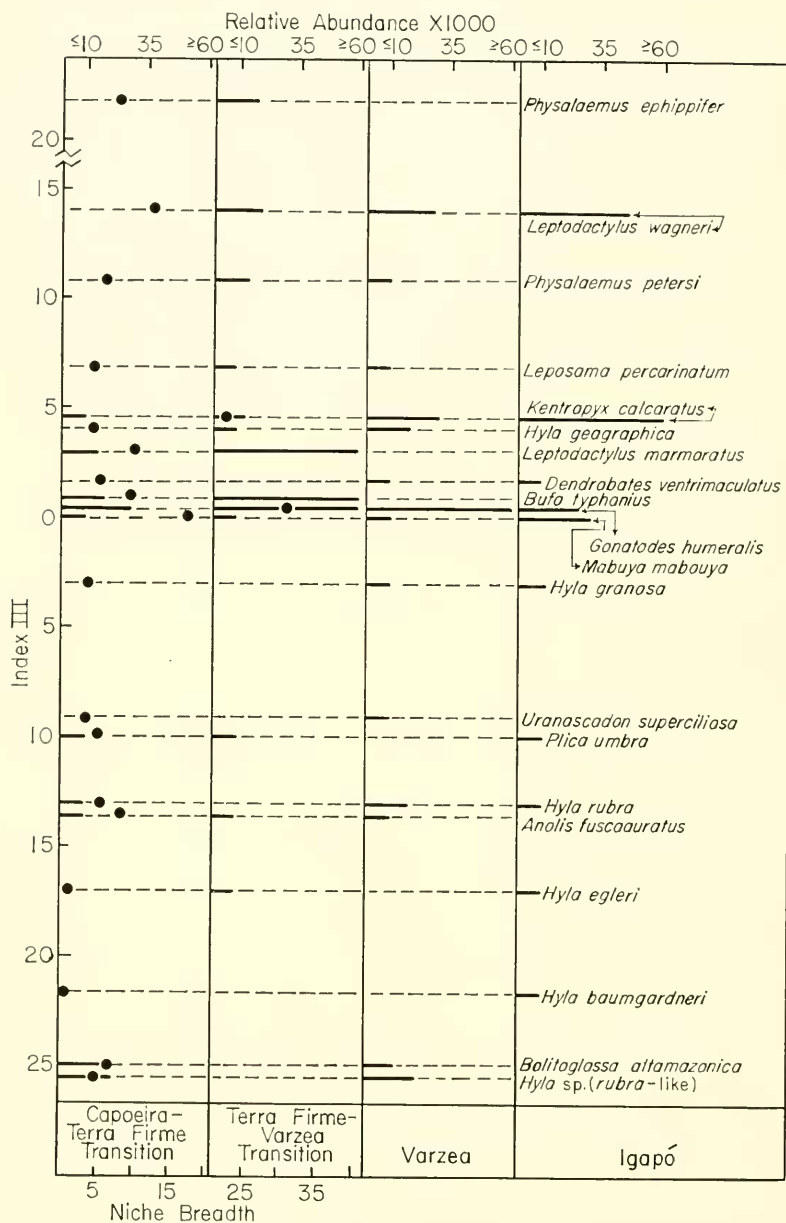


FIG. 24. Relationship of species scores on index III, relative abundance, and niche breadth scores for 20 species in each of the four major areas. See figure 22 for explanation.

NICHE BREADTH ANALYSIS

Niche breadth is used in this paper to refer to habitat niche breadth and is presumed to be correlated with the range of environmental tolerances. Niche breadth scores were calculated from the standard formula proposed by Levins (1967), where p_{ij} is the proportion of occurrences of species j in plot i , niche breadth of species j (B_j) equals:

$$1/B_j = \sum_i p_{ij}^2$$

No actual environmental measurements were taken; resource requirements for each species were measured indirectly by assuming that a given sampling plot provides the necessary resources for the amphibians and lizards found therein. Although the niche dimension is referred to as being habitat, there may be certain latent biotic interactions influencing the distribution of species which are included in the niche breadth measurement. The limitation of using occurrence in sampling plots as an indirect method of measuring requirements of species is acknowledged. However, the analysis is the only one feasible due to the lack of direct physical environmental measurements. The data are from the matrix (plot \times species) used in the contingency table analysis. Niche breadth values are included in table 9. The niche breadth analysis used here was not meant to describe the entire niche of each species, but rather to delimit the spectrum of the habitat dimension of the niche of each species.

Three species of lizards (*Gonatodes humeralis*, *Kentropyx calcaratus*, and *Mabuya mabouya*) have much higher niche breadth scores (16-32) than the next highest species, *Leptodactylus wagneri* (approximately 12). These three species of lizards are found in all four of the major areas, account for 41.8 percent of the entire sample of 1218 individuals, and do not have extreme scores on any of the contingency table indices representing environmental gradients. These lizards are considered to have wide niche breadths with regard to habitat requirements and tolerances and are referred to as habitat-generalists (Fig. 25). The relative abundances in each major area are plotted in figure 26.

Five species can be considered habitat-specialists; all of them have niche breadth scores in the range of 1-4, indicating that they have very narrow tolerances and specialized requirements with regard to the environmental parameters measured indirectly by the analysis (Fig. 25). Each species is found in only one or two of the four major areas and is relatively uncommon. The cumulative

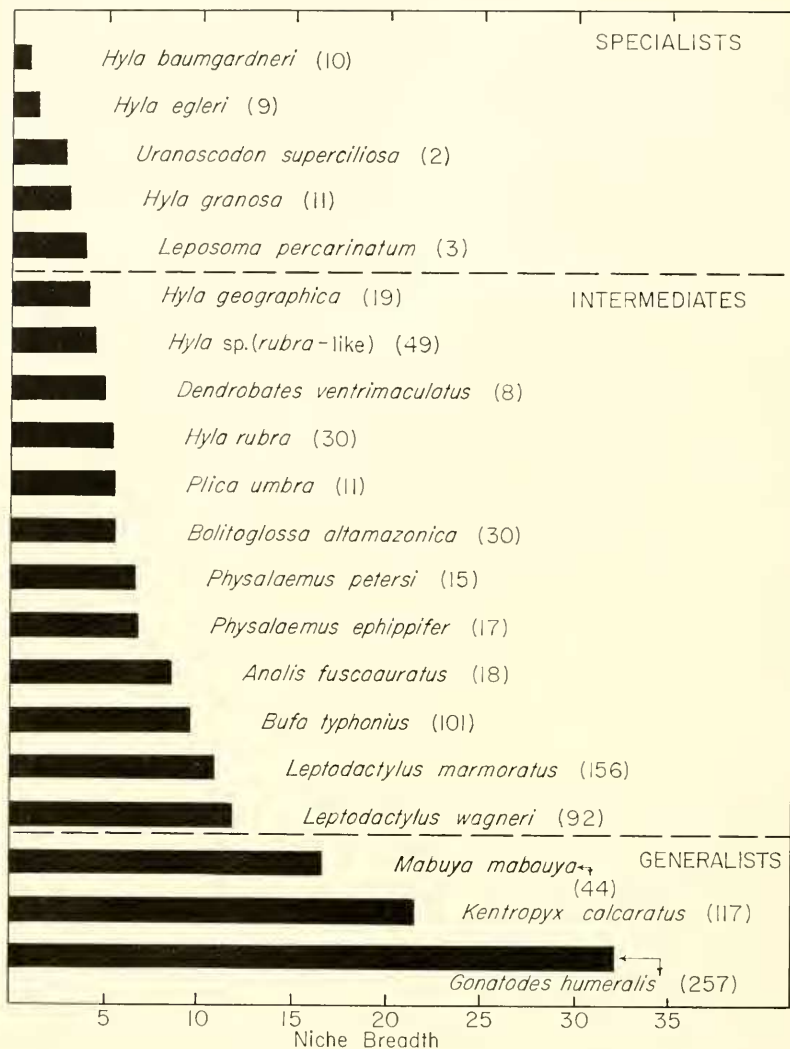


FIG. 25. Niche breadth scores. The bars represent niche breadth scores. Numbers in parentheses indicate the accumulative relative abundance $\times 1000$ in all of the four major areas. The dashed lines separate the species into habitat specialists, intermediates, and generalists.

relative abundance of the five species in all of the areas is only 44 out of the total of 1218 individuals, or 3.6 percent. Two of the habitat-specialists are lizards (*Leposoma percarinatum* and *Uranoscodon superciliosa*), and three are frogs (*Hyla baumgardneri*, *H. egleri*, and *H. granosa*). *Leposoma percarinatum*, a secretive terrestrial lizard found within the leaf litter by day, is probably more

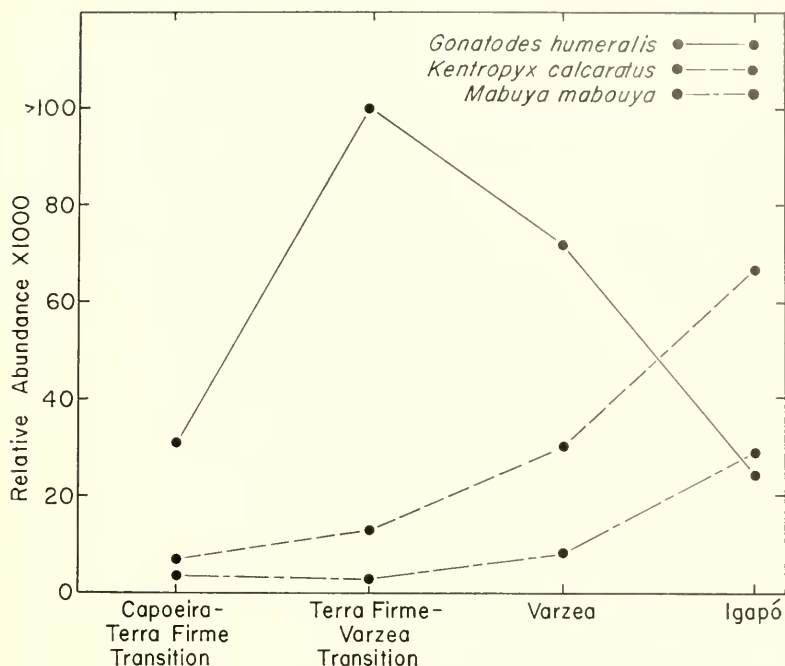


FIG. 26. Relative abundance $\times 1000$ of the three habitat generalists in each of the four major areas.

widely distributed and more abundant than the data indicate. *Uranoscodon superciliosa* is found mainly near pools of standing water in the varzea forest. *Hyla granosa* is predominantly an igapó specialist, not found outside of the forest. The other two species of tree frogs, *H. baumgardneri* and *H. egleri*, are not primarily forest inhabitants, but are found abundantly in open areas; therefore, these two species are not specialized for the particular forest areas, but rather are dependent on standing water. For this reason the species have low niche breadth scores relative to the forest analysis. If a similar study were carried out in open areas, these species would probably have wide habitat niche breadth scores, for they are abundant and seem to have a wide range of environmental tolerances in open areas.

The remaining twelve species are considered to be habitat-intermediates (Fig. 25). In general, these species demonstrate intermediate niche breadth scores, corresponding to relatively few extreme values on the environmental indices from the contingency table analysis. They are generally more abundant and more widely distributed than the habitat-specialists, but less so than the habitat-

generalists. This category includes the one species of salamander, two lizards, and nine frogs. Several of the habitat-intermediates have niche breadth scores similar to those of the habitat-specialists. The artificial line separating the two groups is obviously based on more than niche breadth values; representation and relative abundance in the major areas were also considered.

There seems to be a definite relationship between cumulative relative abundance and niche breadth scores (Fig. 27). In general, those species with wide habitat tolerances (high niche breadth values) are more abundant than those with narrow habitat tolerances. The abundant generalist has the highest niche breadth value, the moderately common generalists have lower niche breadth values, and the five habitat-specialists have the lowest niche breadth values and are extremely uncommon.

Another way of looking at the association is to plot index scores against niche breadth values (Fig. 28). All of the habitat-specialists have positive values on the first index, indicative of wet environments. Three of the habitat-specialists are restricted to open, grassy areas. One of the specialists is terrestrial, and the other four are found predominantly on low vegetation. Three of the specialists have more extreme negative values on the fourth index than does the generalist having a negative value. The relationship of niche breadth values to both index scores and relative abundances within each major area is presented (Figs. 22-24).

When index scores are plotted against relative abundance values for each area, it is possible to characterize the areas with regard to species composition in terms of habitat-generalists, intermediates, and specialists (Figs. 18-21). The capoeira-terra firme transition area provides suitable habitat for the three habitat-generalists (one is moderately common and the other two are relatively uncommon), but the five habitat-specialists are absent. The terra firme-varzea transition area is composed of two habitat-specialists, the three generalists, and numerous habitat-intermediates. One of the generalists is very abundant in this area, and the other two species are relatively uncommon; the two specialists are rare. Both of the specialists are found in one additional major area. The varzea area is represented by the three generalists (one abundant, one moderately common, and one relatively uncommon) and three habitat-specialists (all rare); one of the specialists is restricted to the varzea forest. Two of the generalists are moderately common in the igapo forest, and the third is abundant; three habitat-specialists inhabit the area, only one of which (*Hyla baumgardneri*) is restricted to the

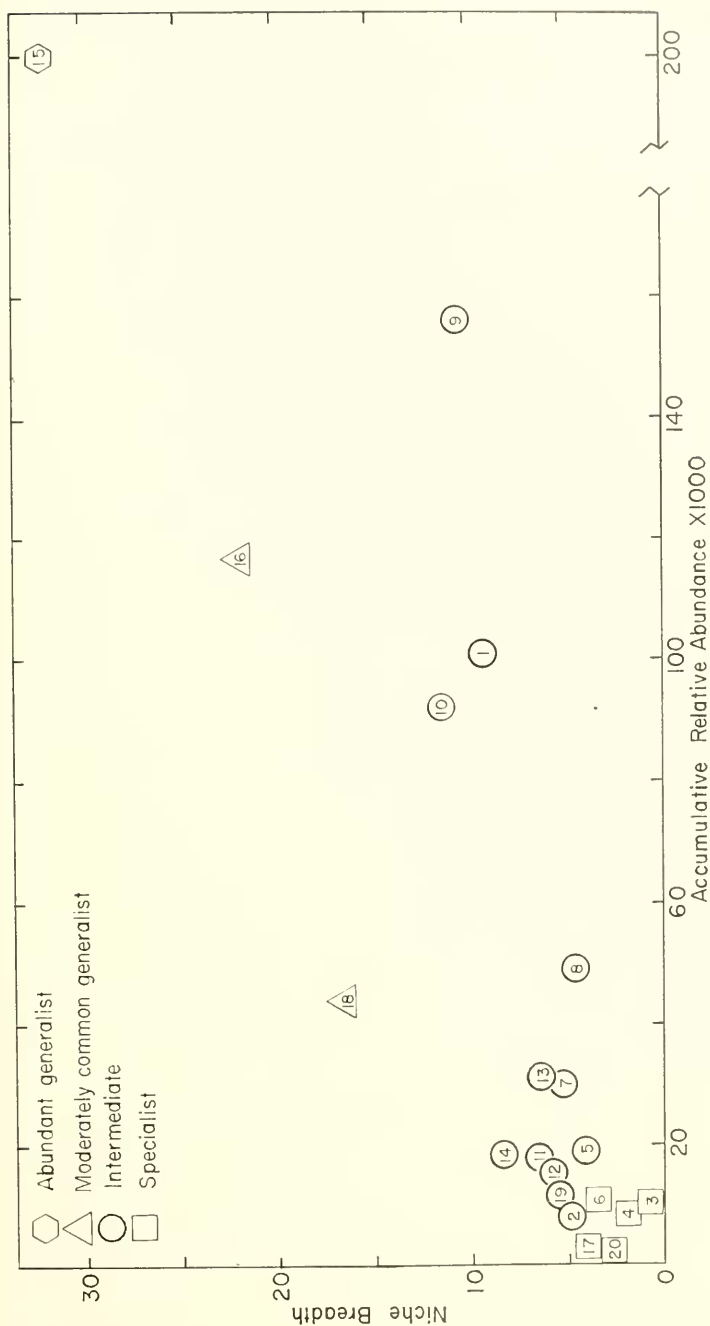


FIG. 27. Accumulative relative abundance $\times 1000$ plotted against niche breadth for each of the 20 species. Species numbers are associated with species names in table 9, p. 29.

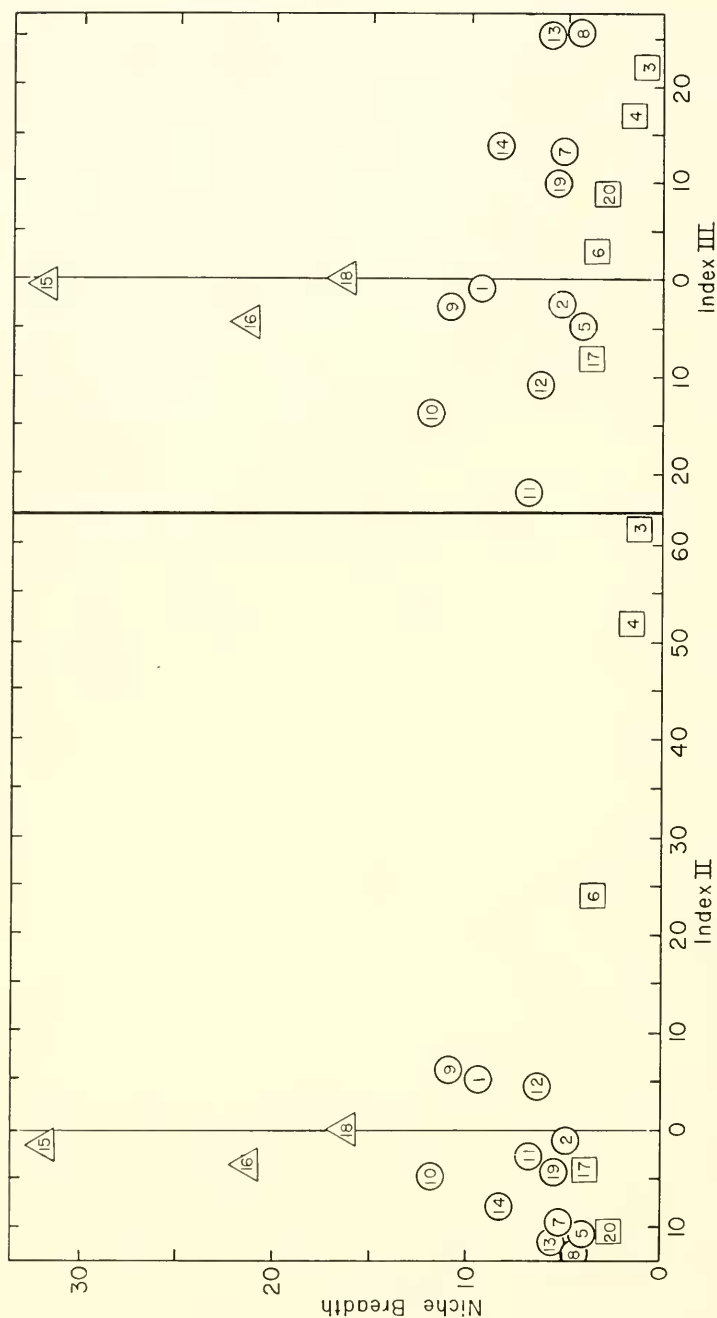


FIG. 28. Species scores on indices II and III plotted against niche breadth for each of the 20 species. Species numbers are associated with species names in table 9, p. 29. Refer to figures 18 and 19 for explanation.

igapó. All three specialists have the highest positive scores of any of the igapó species on the first and second indices, indicating standing water and areas of grassy, emergent vegetation; two species have the highest positive scores on the third index. The habitat-specialists in the igapó forest exhibit more extreme index scores and are more abundant than other specialists in other areas.

NICHE OVERLAP ANALYSIS

In a consideration of niche overlap, it is appropriate to ask: Proportionately, how often do species i and j occur together? Niche overlap can be crudely estimated by plot overlap if we assume that species requirements are intrinsic properties of the plots. The measure does not indicate what the overlapping requirements of the species are, but merely that overlap exists. Niche overlap scores were obtained from a formula suggested by Horn (1966); p_{ij} is the proportion of occurrences of species j in plot i . Overlap of species j and k ($\propto jk$) is then estimated by the following:

$$\propto jk = 2 \sum_i p_{ij} p_{ik} / (\sum_i p_{ij}^2 + \sum_i p_{ik}^2)$$

The index is from 0.0 (no overlap) to 1.0 (complete overlap). A high niche overlap value for two species indicates they are found together in the same plots. For example, *Hyla baumgardneri* and *H. egleri* have an overlap value of 0.971, the highest of any two species associations; these frogs breed in the same plots in the igapó forest. Other high correlations are *Bufo typhonius* and *Leptodactylus marmoratus* (0.928) and *Hyla* sp. (*rubra*-like) and *Bolitoglossa altamazonica* (0.913). Both species pairs usually occur sympatrically and therefore probably overlap greatly with regard to certain environmental requirements.

The following species pairs frequently occur together and have fairly high correlations, likely indicating similarities in environmental requirements: 1) *Kentropyx calcaratus* and *Mabuya mabouya* (0.718); 2) *Hyla rubra* and *Anolis fuscoauratus* (0.631); 3) *Hyla egleri* and *H. granosa* (0.589); 4) *Leptodactylus marmoratus* and *Physalaemus petersi* (0.586); 5) *Leptodactylus marmoratus* and *Gonatodes humeralis* (0.575); 6) *Hyla baumgardneri* and *H. granosa* (0.547); 7) *Leptodactylus wagneri* and *Mabuya mabouya* (0.539); 8) *Hyla rubra* and *Uranoscodon superciliosa* (0.533); 9) *Bufo typhonius* and *Gonatodes humeralis* (0.529); 10) *Anolis fuscoauratus* and *Plica umbra* (0.513); 11) *Hyla geographica* and *Uranoscodon superciliosa* (0.512); and 12) *Bufo typhonius* and

Physalaemus petersi (0.507). *Physalaemus ephippifer* has the least association with any other species, the highest being with *Physalaemus petersi* (0.210). A complete, ordered tabulation of niche overlap values for every species pair combination is given in table 11.

TABLE 11.—Niche Overlap Scores. In each column the species number (see Table 9) is followed by the niche overlap score, as determined by the Horn formula. Scores are ordered within a column; higher numbers indicate a greater degree of overlap.

Species 1	Species 2	Species 3	Species 4	Species 5	Species 6	Species 7
2 0.000	1 0.000	1 0.000	5 0.000	1 0.000	1 0.000	9 0.000
3 0.000	9 0.000	5 0.000	8 0.000	3 0.000	9 0.000	11 0.000
5 0.000	11 0.000	8 0.000	11 0.000	4 0.000	11 0.000	12 0.009
6 0.000	12 0.000	9 0.000	13 0.000	9 0.000	12 0.000	1 0.023
20 0.000	19 0.000	11 0.000	20 0.000	19 0.000	19 0.000	3 0.047
10 0.022	14 0.057	12 0.000	14 0.010	12 0.025	14 0.015	4 0.052
7 0.023	15 0.091	13 0.000	19 0.015	6 0.104	13 0.033	6 0.080
4 0.035	13 0.117	14 0.000	1 0.035	11 0.109	8 0.054	17 0.095
16 0.063	3 0.167	17 0.000	15 0.047	7 0.144	17 0.064	10 0.126
18 0.102	4 0.185	19 0.000	17 0.049	18 0.159	20 0.074	8 0.135
17 0.182	8 0.188	20 0.000	9 0.052	14 0.202	15 0.076	5 0.144
8 0.191	7 0.215	15 0.025	7 0.052	13 0.211	7 0.080	19 0.160
11 0.198	17 0.222	7 0.047	10 0.057	16 0.218	5 0.104	15 0.188
13 0.203	20 0.250	10 0.049	12 0.072	15 0.228	10 0.206	2 0.215
14 0.208	10 0.251	16 0.081	16 0.096	2 0.362	16 0.248	16 0.280
19 0.231	6 0.282	2 0.167	2 0.185	8 0.374	2 0.282	13 0.332
12 0.507	5 0.362	18 0.175	18 0.207	17 0.405	18 0.461	18 0.396
15 0.529	16 0.378	6 0.547	6 0.589	10 0.436	3 0.547	20 0.533
9 0.928	18 0.426	4 0.971	3 0.971	20 0.512	4 0.589	14 0.631

TABLE 11.—Continued

Species 8	Species 9	Species 10	Species 11	Species 12	Species 13	Species 14
3 0.000	2 0.000	19 0.019	2 0.000	2 0.000	3 0.000	3 0.000
4 0.000	3 0.000	1 0.022	3 0.000	3 0.000	4 0.000	11 0.000
11 0.000	5 0.000	9 0.029	4 0.000	6 0.000	11 0.000	4 0.010
12 0.000	6 0.000	14 0.044	6 0.000	8 0.000	12 0.019	6 0.015
6 0.054	7 0.000	3 0.049	7 0.000	20 0.000	6 0.033	10 0.044
9 0.116	20 0.000	4 0.057	8 0.000	7 0.009	10 0.109	2 0.057
10 0.127	10 0.029	11 0.103	13 0.000	13 0.019	2 0.117	17 0.123
7 0.135	16 0.041	13 0.109	14 0.000	5 0.025	9 0.118	12 0.166
16 0.160	4 0.052	7 0.126	20 0.000	18 0.029	17 0.194	9 0.196
2 0.188	18 0.070	8 0.127	18 0.025	16 0.043	16 0.196	5 0.202
1 0.191	8 0.116	12 0.137	10 0.103	19 0.070	1 0.203	1 0.208
17 0.211	13 0.118	20 0.157	5 0.109	4 0.072	5 0.211	18 0.261
20 0.239	11 0.156	6 0.206	16 0.114	10 0.137	20 0.217	16 0.270
18 0.240	19 0.177	2 0.251	17 0.120	14 0.166	18 0.291	8 0.387
15 0.266	14 0.196	17 0.267	9 0.156	11 0.210	15 0.292	15 0.434
19 0.373	17 0.238	15 0.306	19 0.184	15 0.319	7 0.332	13 0.448
5 0.374	15 0.575	5 0.436	15 0.179	17 0.412	19 0.427	20 0.468
14 0.387	12 0.586	16 0.482	1 0.198	1 0.507	14 0.448	19 0.513
13 0.913	1 0.928	18 0.539	12 0.210	9 0.586	8 0.913	7 0.631

SPECIES DIVERSITY AND EQUITABILITY

The Shannon index was used in the present analysis as a means of comparing the four major forest areas. The index is calculated as follows:

$$H' \approx -\sum_i p_i \log p_i \approx C/N (N \log_{10} N - \sum_i n_i \log_{10} n_i),$$

TABLE 11.—*Concluded*

Species 15	Species 16	Species 17	Species 18	Species 19	Species 20
3 0.025	9 0.041	3 0.000	11 0.025	2 0.000	1 0.000
4 0.047	12 0.043	19 0.000	12 0.029	3 0.000	3 0.000
6 0.076	1 0.063	4 0.049	9 0.070	5 0.000	4 0.000
2 0.091	3 0.081	6 0.064	1 0.102	6 0.000	9 0.000
11 0.179	4 0.096	7 0.095	17 0.149	17 0.000	11 0.000
20 0.181	11 0.114	11 0.120	5 0.159	20 0.000	12 0.000
7 0.188	19 0.158	14 0.123	19 0.162	4 0.015	19 0.000
17 0.204	8 0.160	18 0.149	3 0.175	10 0.019	6 0.074
5 0.228	17 0.190	1 0.182	20 0.188	12 0.070	10 0.157
8 0.266	13 0.196	16 0.190	4 0.207	16 0.158	15 0.181
19 0.270	20 0.210	13 0.194	8 0.240	7 0.160	18 0.188
13 0.292	5 0.218	15 0.204	14 0.261	18 0.162	16 0.210
10 0.306	6 0.248	8 0.211	13 0.291	11 0.164	13 0.217
12 0.319	14 0.270	2 0.222	15 0.340	9 0.177	8 0.239
18 0.340	7 0.280	9 0.238	7 0.396	1 0.231	2 0.250
14 0.434	2 0.378	10 0.267	2 0.426	15 0.270	17 0.286
16 0.450	15 0.450	20 0.286	6 0.461	8 0.373	14 0.468
1 0.529	10 0.482	5 0.405	10 0.539	13 0.427	5 0.512
9 0.575	18 0.718	12 0.412	16 0.718	14 0.513	7 0.533

where H' = average diversity per species, p_i = probability of encountering the i^{th} species, C = the constant 3.321928 when using Base 2, N = total number of individuals, and n_i = number of individuals in the i^{th} species. The values are interpreted as follows. If in Area I there are 20 individuals of species A and 20 individuals of species B, then $H' \approx 2.00$; there are two equally common species. If in Area II there are 40 individuals of species A and 10 individuals of species B, then $H' \approx 1.65$; there are 1.65 equally common species. Area I is considered to have a higher species diversity than Area II. The data used were those in the original data matrix which also served as the basis for the contingency table analysis and niche breadth and overlap analyses.

The calculated species diversity values for the four major forest areas are as follows: capoeira-terra firme transition = 3.00; terra firme-varzea transition = 2.45; varzea = 3.02; and igapó = 2.72. Thus, in terms of the sampling plots analyzed, the varzea is the most diverse area with regard to species richness and evenness; the terra firme-varzea transition area is the least diverse. A determination of statistical and biological significance of these values would require additional data, ideally with an equal number of plots sampled per major area.

MacArthur (1957) proposed a "broken-stick model" dealing with species equitability based on one million individuals of 200 species. The model is based on the equation

$$\pi_r = 1/s \sum_{i=1}^r 1/s-i+1),$$

where π_r is the theoretical proportion of individuals in the r^{th} most abundant species ($r = 1, 2, \dots, s$), each theoretical proportion itself being obtained by summing over r terms ($i = 1, 2, \dots, r$). By using this formula, it is possible to obtain an apportionment of the individuals among the species in a sample in about as equitable a manner as ever occurs in nature. An advantage of MacArthur's model is that there is no set of parameters into which data must conform; for each possible number of species (s), the equation generates a complete set of s proportions π_r ($r = 1, 2, \dots, s$). The model yields a curve whereby species abundances are graduated from the rarest to the most common. A maximum equitability curve, whereby for every sample size each species is equally abundant, can also be calculated. Species diversity values (H') obtained from the Shannon index can then be compared to the broken-stick and maximum equitability curves. Any community falling between the two curves is considered to be extremely diverse.

The species diversity values for the four areas were plotted in relation to the curve expected from the broken-stick model and the maximum equitability curve (Fig. 29). All areas fall to the left of the broken-stick distribution with the exception of the capoeira-terra firme transition area; the position of this area suggests that it is highly diverse in terms of species equitability. The validity of this model was questioned by Hairston (1969). He claimed that the broken-stick model lacks ecological meaning, because conformity to the model is largely a function of sample size. He demonstrated that large samples tend to make rare species even more rare and common species even more abundant; the reverse distortion is apparent in small samples. Because of the small sample sizes in the present analysis, the distribution of abundances may be distorted

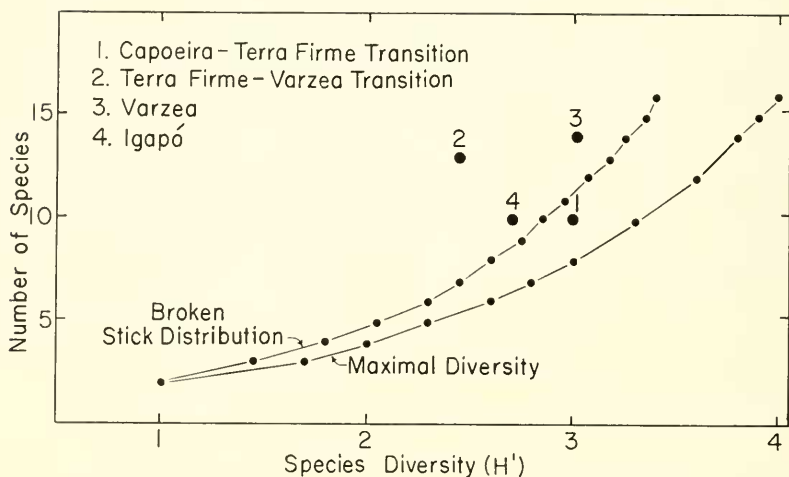


FIG. 29. Relationship of species diversity and numbers of species for each of the four major areas to MacArthur's broken stick distribution and maximal diversity.

such that rare species appear to be more common relative to abundant species than actually is the case.

Lloyd and Ghelardi (1964) proposed an equitability equation for the measure of fit of observed relative abundances of species to those predicted by MacArthur's broken-stick model, as follows:

$$E = s'/s,$$

where s is the actual number of species and s' is the theoretical number of species that should be present according to the broken-stick model at the actual diversity (H'), as calculated from the Shannon index. Maximum conformation to the model is 1.00. The following equitability indices were calculated from Lloyd and Ghelardi's table: capoeira-terra firme transition = 1.10; terra firme-varzea transition = 0.58; varzea = 0.79; and igapó = 0.90. Because of inequity in the distribution of individuals among the species, the sample from the capoeira-terra firme transition forest has a species diversity appropriate to a community with 10 percent more species than actually occur in the particular sample. On the other hand, the samples from the terra firme-varzea transition, varzea, and igapó areas have species diversities appropriate to communities with only 58, 79, and 90 percent as many species as actually occur in the respective areas. Therefore, only the capoeira-terra firme transition area is more diverse than would be expected by the

TABLE 12.—Comparisons of Major Areas by Coefficients of Community. Numbers in Roman are the number of shared species of amphibians and lizards between two major areas; numbers in bold face are the actual number of species in a given area; numbers in italics are the coefficient of community values.

Major Areas	Terra Firme	Varzea	Igapó	Capoeira	Open & Edge
Terra Firme	36	24	16	20	16
Varzea	<i>0.480</i>	38	19	16	18
Igapó	<i>0.381</i>	<i>0.463</i>	22	13	12
Capoeira	<i>0.556</i>	<i>0.381</i>	<i>0.448</i>	20	10
Open & Edge	<i>0.296</i>	<i>0.333</i>	<i>0.273</i>	<i>0.227</i>	34

broken-stick model (Fig. 29). Again, because of small sample sizes, the statistical and biological significance of this analysis is uncertain.

COEFFICIENT OF COMMUNITY

The coefficient of community (CC), used to measure the relative similarity of samples from two communities (major areas), is calculated,

$$CC = S_{ab} / (S_a + S_b - S_{ab}),$$

where S_{ab} is the number of species shared by samples A and B, S_a is the total number of species present in sample A, and S_b is the total number of species present in sample B.

Coefficients were calculated for every two area combinations for five major areas: open and edge areas, capoeira, terra firme, varzea, and igapó. The distribution data used are found in table 2, consisting of 62 species of frogs, salamanders, and lizards. The coefficients are presented in table 12, in addition to the actual number of species every two areas have in common. The varzea and terra firme forests have the most species in common (24), but the coefficient of community is the second highest (0.480). The capoeira and terra firme forests have 20 species in common and have the highest coefficient of community (0.556). The capoeira forest and open and edge areas have the fewest species in common (10) and have the lowest coefficient of community (0.227). Likewise, there is low similarity between the igapó forest and open and edge areas (12 shared species, with a coefficient of 0.273).

SUMMARY AND CONCLUSIONS

The ecological distribution of each of 62 species of frogs, salamanders, and lizards was determined by means of continuous

sampling throughout the environment from mid-January to the end of July, 1969, two weeks in April 1970, and June-July, 1970. Each species exhibits a characteristic distribution, according to its genetic, morphological, and physiological make-up, its life cycle, its way of relating to the physical environment, and its interactions with other species.

The contingency table analysis was used to obtain a measure of the association between species of amphibians and reptiles and their habitats (plots) and to partition this association into independent components (indices) which determine the distribution of species within four of the major forest areas. The components are interpreted as follows: the first is a moisture gradient; the second, a vegetation density gradient; the third, a vertical distribution gradient, and the fourth seems to be a composite of environmental parameters. Each species can be characterized in terms of the indices. Species with scores near zero are the most generalized with regard to the environmental parameters studied and are generally the most abundant species; those species with extremely high positive or low negative scores are restricted to a particular range of the environmental spectrum and are relatively uncommon. The species of frogs exhibit more environmental extremes than do the lizards, indicating that the particular species of frogs studied have more narrow environmental tolerances than do the lizards included in the analysis. The environment likely produces greater restrictions on frogs than on lizards in the carrying out of life processes due to basic physiological differences between the animals, resulting in more restricted distributions for frogs than for lizards.

Niche breadth scores, as calculated from Levins' formula, are presumed to be correlated with the range of environmental tolerances. Three species of lizards have much higher habitat niche breadth scores than the other 17 species of amphibians and lizards; these three species are the only ones found in all of the major forest areas. There is a definite relationship between cumulative relative abundance and niche breadth values. In general, those species with wide environmental tolerances (high niche breadth scores) are more abundant than those with narrow tolerances (low niche breadth scores).

When niche breadth scores, abundance indices, and scores on the environmental gradients are analyzed together, three species are referred to as habitat-generalists, five species as habitat-specialists, and the remaining twelve as habitat-intermediates. The generalists occur in all major areas, have high niche breadth scores, are abundant, and exhibit no extreme scores on the environmental

gradients; the specialists are found in only one or two major areas, have low niche breadth scores, are relatively uncommon, and exhibit extreme requirements on one or more environmental gradient.

Partitioning of resources is evident, in terms of both space and time. One of the most striking examples is the calling site segregation among breeding male frogs in a given area. Habitat niche overlap can be estimated by plot overlap. Many species pairs have relatively high overlap values, thereby indicating that they frequently occur in association with each other. Assuming the plot is indicative of the requirements and tolerances of the species found therein, we can conclude that some niche overlap does exist.

Four of the major forest areas were compared and contrasted by various analytical techniques. Each area was characterized by the contingency table indices. The capoeira-terra firme transition area is relatively dry and has rather dense vegetation; the herpetofauna predominantly inhabits low vegetation and tree trunks. The terra firme-varzea transition area can be divided into high ground transition and low, wet transition. The entire transition zone is an intermediate area with respect to the environmental gradients, except that in many areas the ground cover is less dense than that of the capoeira-terra firme transition area. The varzea plots are relatively wet and have fairly dense ground cover. The igapó forest is the wettest area and has intermediate to relatively dense ground cover; most of the lizards are either terrestrial or are found on the boardwalks, and the frogs are found both on low vegetation and on the ground.

Another way of comparing the areas is in terms of species richness and equitability. Species richness values for five major areas are: varzea—38 species; terra firme—36 species; open and edge areas—34 species; igapó—22 species; and capoeira—20 species. Coefficients of community were calculated on these data to determine relative similarity between every two areas. The highest similarity is between capoeira and terra firme forests (0.556), and the lowest is between capoeira and open-edge areas (0.227). Species diversity (Shannon index) scores were calculated from the contingency table data matrix; the results are: varzea—3.02; capoeira-terra firme transition—3.00; igapó—2.72; and terra firme-varzea transition—2.45. Equitability values were then calculated from the species diversity estimates (H') and compared to MacArthur's broken-stick model. The capoeira-terra firme transition area has an equitability of 1.10, indicating that the area is more diverse than would be expected by MacArthur's model. As dis-

cussed in the relevant section, the statistical and biological significance of this analysis is uncertain due to small sample size.

The ecological requirements and tolerances characteristic of species in a community vary widely. Every species exploits the available resources in the most effective way possible for that particular species. Some species accomplish this by specializing in part of the environment, whereas others are generalized and utilize a greater spectrum of environmental parameters. It is concluded that the niche segregation existent among the frogs, salamanders, and lizards living in various habitats within the rainforest at Belém permits many species to coexist with highly efficient utilization of environmental resources.

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LITERATURE CITED

- BELÉM VIRUS LABORATORY, BELÉM, PARÁ, BRAZIL
1967. Annual report. Unpublished.
- CAIN, S. A., G. M. DE O. CASTRO, J. M. PIRES, and N. T. DA SILVA
1956. Application of some phytosociological techniques to Brazilian rain forest. *Amer. J. Botany*, 43:911-941.
- DUELLMAN, W. E.
1967. Courtship isolating mechanisms in Costa Rican hyliid frogs. *Herpetologica*, 23:169-183.
- HAIRSTON, N. G., J. D. ALLEN, R. K. COLWELL, D. J. FUTUYMA, J. HOWELL, M. D. LURIN, J. MATHIAS, and J. H. VANDERMEER
1968. The relationship between species diversity and stability: an experimental approach with Protozoa and bacteria. *Ecology*, 49(6):1091-1101.
- HATHEWAY, W. H.
1967. Physiognomic characterizations of three vegetational types at the Guamá Ecological Research Area, Belém, Brazil. Unpublished report to the Smithsonian Institution, June 15, 1967:1-35.
- HORN, H. S.
1966. The measurement of "overlap" in comparative ecological studies. *Amer. Nat.*, 100:419-424.
- HUTCHINSON, G. E.
1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology, 22:415-427.
- INGER, R. F. and B. GREENBERG
1966. Ecological and competitive relations among three species of frogs (genus *Rana*). *Ecology*, 47(5):746-759.
- KENDEIGH, S. C.
1961. Animal ecology. Prentice-Hall, Inc., Englewood Cliffs, N.J., 468 pp.
- LLOYD, M. and R. J. GHELARDI
1964. A table for calculating the "equitability" component of species diversity. *J. Animal Ecol.*, 33:217-225.
- LLOYD M., R. F. INGER, and F. W. KING
1968. On the diversity of reptile and amphibian species in a Bornean rain forest. *Amer. Nat.*, 102(928):497-515.
- MACARTHUR, R. H.
1957. On the relative abundance of bird species. *Proc. Natl. Acad. Sci. U.S.*, 43:293-295.
1964. Environmental factors affecting bird species diversity. *Amer. Nat.*, 98:387-398.
1965. Patterns of species diversity. *Biol. Rev.*, 40:510-533.

- MACARTHUR, R. H. and J. W. MACARTHUR
1961. On bird species diversity. *Ecology*, 42:594-598.
- MACARTHUR, R. H., J. W. MACARTHUR, and J. PREER
1962. On bird species diversity: II. Prediction of bird census from habitat measurements. *Amer. Nat.*, 96:167-174.
- MACARTHUR, R. H., H. RECHER, and M. CODY
1966. On the relation between habitat selection and species diversity. *Amer. Nat.*, 100:319-332.
- PIANKA, E. R.
1967. Lizard species diversity. *Ecology*, 48(3):333-351.
- PIELOU, E. C.
1966. Shannon's formula as a measure of specific diversity: its use and misuse. *Amer. Nat.*, 100:463-465.
- RAND, A. S.
1964. Ecological distribution in anoline lizards of Puerto Rico. *Ecology*, 45:745-752.
- RAND, A. S. and S. S. HUMPHREY
1968. Interspecific competition in the tropical rain forest: ecological distribution among lizards at Belém, Pará. *Proc. U.S. Natl. Mus.*, 125(3658):1-17.
- SCHOENER, T. W.
1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology*, 49:704-726.
1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology*, 51(3):408-418.
- SCHOENER, T. W. and G. C. GORMAN
1968. Some niche differences in three Lesser Antillean lizards of the genus *Anolis*. *Ecology*, 49(5):819-830.
- SHANNON, C. E.
1948. The mathematical theory of communication. In C. E. Shannon and W. Weaver, *The mathematical theory of communication*. Univ. Illinois Press, Urbana, 117 pp.
- WHITTAKER, R. H.
1970. *Communities and ecosystems*. The Macmillan Company, Collier-Macmillan Limited, London, 162 pp.
- WILLIAMS, E. J.
1952. Use of scores for the analysis of association in contingency tables. *Biometrika*, 39:274-289.